MEMOIRS OF THE QUEENSLAND MUSEUM



MEMOIRS

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CONTENTS

	Page
ARMSTRONG, J. D. and Brown, C. D. A New Species of Attenuatella from the Permian of Queensland	59
BARTHOLOMAI, ALAN A New Fossil Koala from Queensland and a Reassessment of the Taxonomic Position of the Problematical Species, Koalemus ingens De Vis	65
CROSBY, ELEANOR An Archaeological Site Survey near Taroom, South-Eastern Queensland	73
Stephenson, W. Variability in the Sand Crab Portunus pelagicus (Linnaeus) (Crustacea: Portunidae)	83
STEPHENSON, W. and REES, MAY A Revision of the Charybdis miles "Group" of Species (Crustacea: Portunidae), with Description of a New Species from Queensland Waters	91
WOODS, JACK T. The Identity of the Extinct Marsupial Genus Nototherium Owen	111

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A NEW SPECIES OF *ATTENUATELLA* (BRACHIOPODA: SPIRIFERIDA). FROM THE PERMIAN OF QUEENSLAND.

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and

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ABSTRACT

Attenuatella australis sp. nov. is described from the siltstone unit underlying the Gigoomgan limestone in the Maryborough Basin, Queensland. The species occurs with invertebrates typical of the Tiverton Formation in the Bowen Basin and is thus probably of Lower Artinskian (Aktastinian) age.

The species described in this paper occurs about 600 feet below the base of the Gigoomgan limestone (Richards and Bryan, 1932, p. 295) in the Maryborough Basin, and it is associated with a fauna that includes *Anidanthus springsurensis* (Booker), *Cancrinella farleyensis* (Etheridge and Dun), *Ingelarella ovata* Campbell, and *I. profunda* Campbell. This fauna is correlative with that in the Tiverton Formation in the Bowen Basin (Dickins's (1964) Fauna II), and is probably of Lower Artinskian (Aktastinian) age (Dear, 1966; Armstrong *et al.*, 1967; Dickins, in press). The specimens of *Attenuatella australis* sp. nov. were collected by Brown and first recorded and described in an unpublished manuscript by Brown (1964).

Outside Australia, *Attenuatella* Stehli occurs in the Permian of Russia, North America, New Caledonia, and New Zealand (Landis & Waterhouse, 1966) and its known range is from the Artinskian to the lower part of the Upper Permian.

All the figured specimens of *Attenuatella australis* sp. nov. are housed in the Department of Geology and Mineralogy, University of Queensland and are designated by a number prefixed by UQF. Topotypic material has been lodged in the collections of the Queensland Museum,

Subfamily AMBOCOELIINAE George, 1931 Genus Attenuatella Stehli, 1954

TYPE SPECIES (by original designation): Attenuatella texana Stehli (1954, p. 343, pl. 25, figs 31–33) from the Lower Leonardian, Bone Spring Formation, Texas.

Attenuatella australis sp. nov. (Fig. 1; pl. 8, figs. 1-16.)

HOLOTYPE: UQF52677 from about 600 feet below the base of the Gigoomgan limestone in the Maryborough Basin, Queensland. The holotype is from a locality one mile north-east of Gigoomgan homestead, about 33 miles west-south-west of Maryborough, Queensland.

DIAGNOSIS: Ventral valve strongly inflated with a narrow sulcus for its entire length; umbo incurved for up to one-quarter of the valve length; in profile the umbo is ventral to the commissural plane; dorsal valve convex rostrally, but concave near the commissure; on its posterior third the valve bears two low diverging folds; microornament on both valves of spines, 7 to 10 per millimetre arranged in obscurely concentric lines; ventral diductors elongate, located on the inner slopes of ridges bordering the posterior part of the adductor area.

DESCRIPTION: The shell is concavo-convex with a broadly uniplicate commissure. It has an elongate inflated ventral valve, and an approximately semi-circular reflexed dorsal valve. The ventral umbo is high, narrow, and variably incurved but in profile does not attain the level of the commissure (fig. 1: A, B, C). Only the tip of the beak is inrolled, and from the posterior edge of the shell the beak may extend forwards for up to one-quarter of the shell length. The specimen of A. australis having the most inrolled umbo is shown in plate 8, fig. 10, whereas the umbones of the holotype and the specimen in plate 8, fig. 8 are typical of the majority of specimens of the species. The ventral area is strongly curved apically and at the hinge line is almost perpendicular to the commissural plane. There is a narrow but distinctive sulcus for the entire length of the valve; otherwise the flanks of the valve are smooth. Cardinal extremities are obtusely rounded, and the greatest shell width is in front of the hinge The dorsal area is catacline and is only one-quarter as high as the ventral area. The dorsal valve is gently convex rostrally but becomes flattened and then distinctly concave towards the commissure. A pair of low folds diverge antero-laterally from the beak. The folds occur only on the posterior convex part of the valve and between them there is a shallow depression. The shape of the valve is somewhat variable as in Attenuatella incurvata Waterhouse (1964, pl. 20, figs 10-12). Both valves of A. australis are covered with obscurely concentric lines, about 0.2 mm apart, of fine cylindrical spines, and along each line there are 7 to 10 spines per millimetre. A small groove runs towards the commissure for a short distance from each spine (plate 8, fig. 16).

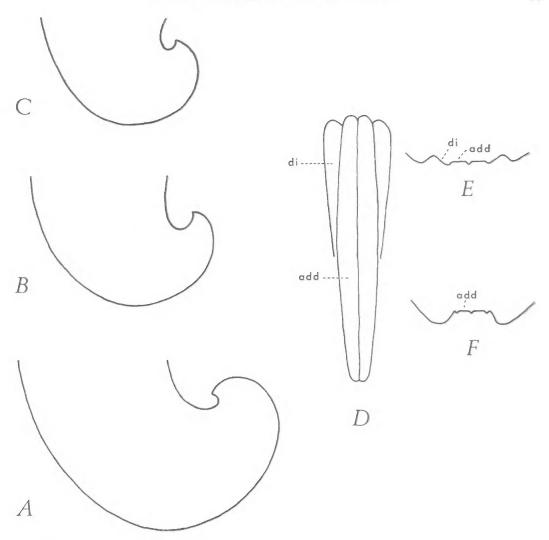


Fig. 1: Attenuatella australis sp. nov.

- A, B, C. Camera lucida drawings of lateral views of three ventral valves, UQF46648, UQF52676, and UQF52679 respectively $(\times 4.75)$.
- D. Diagrammatic representation of the muscle field in the ventral valve; di, diductor attachment area; add, adductor attachment area (approx. × 7.5).
- E, F. Sections through the posterior and anterior parts respectively of the ventral muscle field.

In the ventral valve the area of muscle attachment is posteriorly a depressed region between two prominent ridges, and anteriorly a raised platform with small ridges along its sides (fig. 1: D, E, F). The diductors were attached to the inner

slopes of the ridges and extended for a half to two-thirds of the length of the platform. The areas of adductor attachment occupied the entire length of the platform. Adductor and diductor fields were separated by small grooves and a narrow depression divided the adductor areas. A delthyrial plate occupies the apical third of the delthyrium but is not depressed below the level of the area.

The cardinal process is tuberculate and lies between the posterior ends of the inner socket ridges (plate 8, figs 1, 2). These ridges are confluent with the crural bases. The shell is impunctate.

DISTRIBUTION: Attenuatella australis is known only from the type locality.

AGE: Lower Permian, probably Lower Artinskian (Aktastinian).

COMPARISON: Attenuatella australis differs from A. texana Stehli (Stehli, 1954, p. 343, pl. 25, figs 31-33) of Lower Leonardian age in having a more distinct median depression in the ventral valve. The Wordian species A. attenuata (Cloud) (Cloud, 1944, pp. 62-3, pl. 17, figs 22-25) has a more inrolled beak, a gently convex dorsal valve and a less obvious ventral sulcus. A. incurvata Waterhouse (Waterhouse, 1964, pl. 20, figs 1-12, pl. 21, figs 1-9) of possible Kazanian age may be distinguished by its less prominent ventral sulcus, generally narrower, more posteriorly elongate ventral valve, and more incurved beak. In A. australis the ratio of the length of the incurved part of the ventral valve to the length of the shell is less than one-quarter, whereas in A. incurvata it is about one-third; generally only the tip of the beak is inrolled in A. australis. Moreover in A. australis the ventral umbo is always ventral to the commissural plane whereas in A. incurvata it reaches or is dorsal to this plane (Waterhouse, 1964, pl. 20, figs 2 and 11). The incurved part of the umbo of Attenuatella sp. figured by Waterhouse (1966, pl. 1, figs 1-5) from the Wesney Silkstone in the Eglinton Volcanics in New Zealand is also relatively small but this species has a flat costate dorsal valve and an almost imperceptible sulcus in the ventral valve. The species A. acutirostrus (Krotova) (Krotova, 1885, pl. 4, fig. 24) from the Artinskian of Russia is perhaps most similar to A. australis; however the former species has a very distinct sulcus in the ventral valve.

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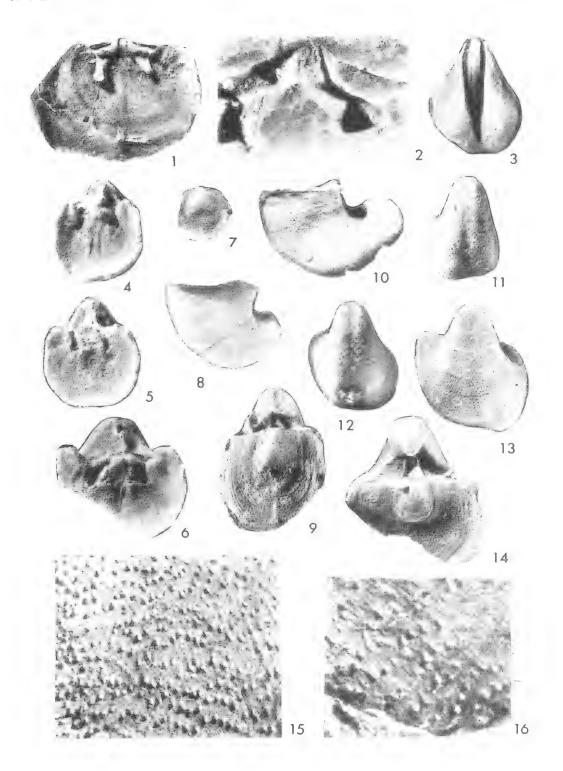
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PLATE 8

Attenuatella australis sp. nov.

- Fig. 1: Interior of dorsal valve, UQF46647.
- Fig. 2: Dorsal cardinalia showing tuberculate cardinal process, UQF46647, \times 10.
- Fig. 3: Internal mould of ventral valve, UQF52673.
- Figs 4, 5, 6: Views of internal moulds of three dorsal valves, UQF52674, UQF52675, UQF46778, respectively.
- Fig. 7: Exterior of dorsal valve, UQF46646.
- Figs 8, 13: Lateral and ventral aspects of ventral valve, UOF52676.
- Fig. 9: Dorsal view of holotype, UQF52677.
- Figs 10, 14: Lateral and dorsal views of UQF46648.
- Figs 11, 12: Exteriors of two ventral valves, UQF52678 and UQF52679, respectively.
- Fig. 15: Micro-ornament of granules on UQF52676, approx. × 16.
- FIG. 16: Micro-ornament of granules and grooves on UQF52680, approx. × 25. The granules are not hollow, the appearance in the figure being produced by bubbles in the casting medium.

All figured specimens are from the same locality as the holotype and all figures are \times 4 unless otherwise stated.





A NEW FOSSIL KOALA FROM QUEENSLAND AND A REASSESSMENT OF THE TAXONOMIC POSITION OF THE PROBLEMATICAL SPECIES, KOALEMUS INGENS DE VIS

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ABSTRACT

A new species of fossil koala, *Phascolarctos stirtoni*, is described from the cave and fissure fill deposits of the Cement Mills limestone quarry, south-eastern Queensland, together with a discussion on the taxonomic position of the supposed koala, *Koalemus ingens* De Vis, which is considered to be referable more likely to the Diprotodontidae.

The presence of fossil marsupials in cave and fissure fill deposits in Queensland has been noted by Longman (1925, 1945) and Woods (1960), material having been derived from the limestone quarries at Marmor, south-east of Rockhampton, and Cement Mills, near Gore, south-west of Warwick. In addition, Woods (1960) has recorded bone from caves in the vicinity of Mt. Etna, near Rockhampton, and from Mingoola and Glenlyon, between Texas and Wallangarra.

While several marsupials, of both extinct and extant species have been reported from the occurrence at Cement Mills, the faunal list is by no means complete, and this study presents the first evidence of the existence of phalangerid remains in the deposits.

A supposed fossil koala, *Koalemus ingens* has already been recorded from the Upper Cainozoic fluviatile deposits of south-eastern Queensland. This, however, appears to have been derived most likely from one of the smaller diprotodontids of the Chinchilla Sand, of possible Pliocene age.

A copy of the data treated statistically in this study has been lodged in the library of the Queensland Museum. All measurements throughout are in millimetres.

Phascolarctos stirtoni* sp. nov.

(Pl. 9, figs 1-3)

MATERIAL: F5707, holotype, partial right maxilla with P³ – M², juvenile, Cement Mills, near Gore, south-east Queensland, of Pleistocene age.

DIAGNOSIS: Considerably larger than the living *Phascolarctos cinereus* (Goldfuss); P^3-M^2 with strong accessory ridges and molars with strong lingual ridge across extremity of median valley.

DESCRIPTION: Known only from $P^3 - M^2$.

P3 moderately large, elongate, its length being slightly less than that of M1, subovate in basal outline, broader posteriorly than anteriorly. Crown with moderately low, sinuous longitudinal crest and low, anteriorly convergent lingual cingulum, confining a moderately broad lingual basin; longitudinal crest highest posteriorly, transected by two sets of vertical labial and lingual ridges between the anterior and posterior cusps; cuspules produced at crest; extensions of longitudinal crest extend postero-lingually towards crown base, and anteriorly to high anterior cuspule; anterior extension ornamented by single, vertical, lingual ridge between cuspule and anterior cusp; labial and lingual ridges descend from anterior cuspule. Lingual cingulum incomplete posteriorly, slightly raised mesially and anteriorly united with lingual ridge from between anterior ridge and cuspule; lingual ridge from posterior cusp of longitudinal crest also unites with lingual cingulum. Labial ridges from posterior and anterior cusps of crest descend towards crown base. Lingual basin crossed by extensions of ridges from cuspules and anterior cusp of longitudinal crest, and mesially by strong ridge from elevated portion of lingual cingulum; minor ridges also present anteriorly and posteriorly across lingual basin.

 $\rm M^1 < M^2$; molars subselenodont, broad, subrectangular in basal outline, with labial and lingual margins somewhat convergent posteriorly; anterior breadth of $\rm M^1$ slightly greater than that of $\rm M^2$. Cusps low, sharply defined. Paracone with well-defined angular ridges; one descends antero-labially to extremity of crown at junction of low anterior cingulum and slight labial cingulum, another curves postero-labially to unite with raised portion of labial cingulum at cuspule at extremity of median valley, while another descends postero-lingually into median valley; subdued ridge descends antero-lingually; labial and posterior surfaces concave while antero-lingual aspect generally convex, giving paracone a subcrescentic appearance; variable accessory ridges descend anteriorly and lingually and to a lesser degree posteriorly. Protocone with well-defined angular ridges; one descends antero-labially to unite with anterior cingulum lingual to axis of crown, another curves postero-labially to unite with antero-labial

^{*} Named for the late Professor R. A. Stirton, who did so much to stimulate recent work on Australian fossil marsupials.

ridge from hypocone, above median valley; lesser ridge descends labially, subdivides labial concave surface of cusp; slight variable ridge descends antero-lingually to crown margin, from protocone or from its antero-labial ridge, occasionally unites with lingual, discontinuous extension of anterior cingulum, and anterior margin of moderately high, short, lingual cingulum; antero-lingual aspect of cusp generally convex, giving cusp a subcrescentic appearance; variable accessory ridges at base of cusp surfaces developed anteriorly, lingually and postero-lingually. Metacone with well-defined angular ridges; one descends antero-labially to raised portion of labial cingulum at cuspule at labial extremity of median valley, another postero-labially to margin of crown, uniting with extremities of labial and low, posterior cingula; labial aspect of cusp concave, while lingual aspect convex, giving cusp a crescentic appearance; variable accessory ridges descend antero-lingually, lingually and particularly postero-lingually. Hypocone with well-defined angular ridges; one descends antero-labially to unite with postero-labial ridge from protocone, and another curves postero-labially to unite with posterior cingulum above axis of crown; lesser ridges descend antero-lingually to unite with posterior limit of lingual cingulum, and labially, subdividing concave labial surface of cusp; lingual aspect of cusp generally convex, giving hypocone a subcrescentic appearance; variable accessory ridges developed antero-lingually and lingually towards bases of cusp surfaces. Strong, ornamented accessory ridges developed sub-parallel to crown axis from anterior cingulum, between paracone and protocone, while variable transverse ridges developed in labial moiety of median valley. Fossettes developed anterolingually, and in lingual moiety of median valley.

DISCUSSION: Many of the early specimens collected from Cement Mills were from unconsolidated or consolidated reddish cave earths. Recently collected material, including the holotype of *Phascolarctos stirtoni*, are almost invariably from consolidated cave and fissure fill in the Palaeozoic Cement Mills limestone. It is probable that some age differences exist, but the deposits at present show no evidence of stratification, and no precise information is available regarding the disposition of the specimens within the deposit. A Pleistocene age is presumed for the Cement Mills material, because of the reasonably high proportion of extinct species, but because of the presence of species still extant, at least some of the deposit may have accumulated during the late Pleistocene.

P. stirtoni is somewhat similar morphologically to the modern koala, P. cinereus (Goldfuss). It lacks a postero-labial cuspule on P³ and has its longitudinal crest only slightly sinuous. However, the cuspule is sometimes absent in P. cinereus and while the crest is usually markedly sinuous in that species, it is variable in this feature. Accessory ridges in P³ and the anterior molars in P. stirtoni are stronger than is usual in P. cinereus, while the ridge across the lingual margin of the median valley of the molars is stronger. The antero-lingual fossette present in the molars of P. stirtoni, is generally absent in P. cinereus.

TABLE 1

Measurements for *Phascolarctos stirtoni* sp. nov., and summary of measurements for *P. cinereus* (Goldfuss)

Character Character	Holotype P. stirtoni			P. cinereus—Summary of Measurements				
			N	OR	$\overline{\mathbf{X}}$	s	V	
P ³ length		9.7	41	6.7-8.3	7.3	0.3931	5.4	
breadth posteriorly		-	42	4.7-5.7	5.1	0.2934	5.8	
M¹ length		10.8	42	7.3-8.7	8.0	0.3639	4.5	
breadth protoloph		10.4	42	7-1-8-2	7.7	0.2922	3.8	
M ² length		10.7	. 45	7.2-8.2	7.7	0.2594	3.4	
breadth protoloph		11.2	46	7-3-8-8	8.0	0.3051	3.8	

In size, however, *P. stirtoni* is considerably larger than *P. cinereus*, as can be seen from the accompanying table of measurements, the fossil exceeding by more than one-third the mean values for the recent species in the sizes of its teeth. This is graphically illustrated in Figure 1. Size differences are apparent between study skins of the southern and northern subspecies of *P. cinereus*, but there are no significant differences in the dimensions of the teeth. Although the sample of the Victorian koala was insufficient for statistical consideration, measurements for individuals fall well within the limits of the Queensland subspecies, *P. c. adustus*.

Stephenson (1963) has argued that intra-specific isometric growth gradients may have played an important role in the evolution of Australian marsupials and monotremes, and that the Quaternary decrease from Pleistocene to Recent forms may be as much as 20–25 per cent. Even allowing for the fact that *P. stirtoni* cannot be compared statistically with the living koala, it is apparent that the size difference alone is too great for this to be considered as simply intra-specific variation.

Glauert (1910) records the presence of the modern koala, *P. cinereus*, in the Pleistocene deposits of the Mammoth Cave, in south-western Western Australia. His measurements for this material conform with those for the recent sample.

A fossil phalangerid of somewhat doubtful affinities, *Perikoala palankarinnica*, was described by Stirton (1957) from the Palankarinna fauna of the possibly early Pliocene Mampuwordu Sands of the Tirari Desert, Lake Eyre Basin, South Australia, but was later referred to the Upper Oligocene Ngapakaldi fauna (Stirton *et al.*, 1961). While this cannot be compared morphologically by direct means with *P. stirtoni*, being based on a partial left mandibular ramus with $P_3 - M_2$, it is considerably smaller than *P. cinereus*, and is obviously generically distinct.

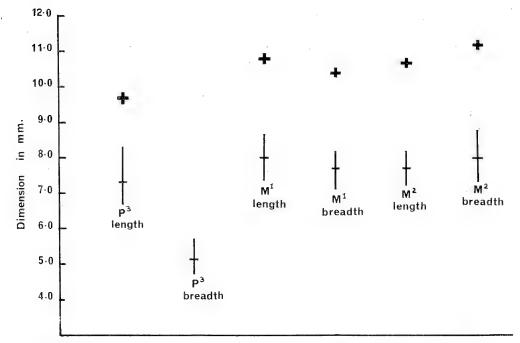


FIG. 1: Comparison of measurements of *Phascolarctos stirtoni* sp. nov. and *P. cinereus* (Goldfuss), with heavy crosses for *P. stirtoni*; light vertical lines represent observed ranges, while horizontal bars represent position of sample means of *P. cinereus*.

THE TAXONOMIC POSITION OF KOALEMUS INGENS DE VIS. 1889

Since its description, *Koalemus ingens* De Vis, has remained something of an enigma in the fauna from the Upper Cainozoic fluviatile deposits of the Darling Downs area, south-eastern Queensland. The holotype, F683, the distal end of an incomplete right fibula, unfortunately lacks precise locality information. However, it is heavily mineralised, hard and stained by oxides of iron, suggesting a likely provenance within the Chinchilla Sand, of possible Pliocene age.

It was fully described by De Vis (1889), and its resemblance with the fibula of the modern koala, *P. cinereus*, was noted. De Vis considered the specimen as a left fibula when, in fact, it comes from the right limb. Beside its moderately large size, the main morphological characters presented by the holotype include a deep, semilunate, external, lateral surface of the epiphysis, this being bounded anteriorly by an expanded, somewhat posteriorly rotated process and posteriorly by a much reduced process. The antero-lateral surface of the epiphysis is also expanded, but the postero-lateral and posterior surfaces are nearly planar. Loss of bone has occurred on other lateral epiphysial surfaces. In distal view, the epiphysis generally slopes postero-mesially,

and is marked by a postero-lateral depression below the postero-lateral process. A shallow depression delimiting the elevated antero-lateral process is also present. Mesially, the surface is broadly convex, the convexity increasing anteriorly. The shaft is subquadrate in section and is moderately strong. It is flattened externally and posteriorly, these surfaces meeting in an angular ridge which continues distally to the postero-lateral epiphysial process. The other surfaces of the shaft are rounded, with a broad ridge ascending from the antero-lateral epiphysial process and a short, broad ridge ascending postero-mesially.

While a general structural resemblance does exist between the fibulae of *K. ingens* and *P. cinereus*, numerous differences are apparent. In particular, the anterolateral process in *P. cinereus* is less expanded in both external and distal views, and is not as rotated as in *K. ingens*. The semilunate lateral aspect is more constricted, while in distal view, the antero-lateral process is isolated by a deep, broad groove. The shaft lacks the postero-lateral angularity visible in *K. ingens*, and anteriorly bears a somewhat angular, longitudinal ridge.

As a supplement to his original description, De Vis (1889) described and referred to K. ingens a left premaxilla and attached partial maxilla. This cranial fragment, F684, again lacks detailed locality information, but appears to have been derived from the Chinchilla Sand, by its preservation. It is definitely referable to a koala, and indicates a size difference of about one-half as large again as P. cinereus. The fibula described as K. ingens is about twelve times as large as that in the recent koala, and this prompted De Vis to estimate the weight of the animal as five hundred-weight or more.

De Vis (1889) attempted to explain the discrepancies in size between the two by suggesting that the cranial fragment had been derived from a juvenile individual. This, however, is not the case because of the extensive wear facets present on I³ and C¹, the only teeth retained in the specimen, and by the nature of the premaxilla-maxilla suture. In size, this fragment compares favourably with *P. stirtoni*, but insufficient evidence is present for its relationship to be considered at this time.

Since, in general, in the Darling Downs deposits, post-cranial remains of marsupials have not been found associated with cranial remains, upon which most of the species are based, any reassessment of the taxonomic position of *K. ingens* must, of necessity, be fairly broad. On the basis of size and morphology, only the families Vombatidae and Diprotodontidae bear consideration.

Only *Phascolonus gigas* Owen, among the Vombatidae, is sufficiently large to warrant comparison. However, the fibula of this species is known, having been described by Stirling (1913), and is quite distinct from that of *K. ingens*.

Among the Diprotodontidae only the smaller forms of the Chinchilla Sand, namely *Euowenia* De Vis and *Palorchestes* Owen, could presumably have accounted for an adult fibula, the size of that of *K. ingens*.

It is believed that reference of *K. ingens* to the Diprotodontidae, regardless of the fact that it cannot be associated with a particular species, is preferable to its present taxonomic assignment within the Phalangeridae.

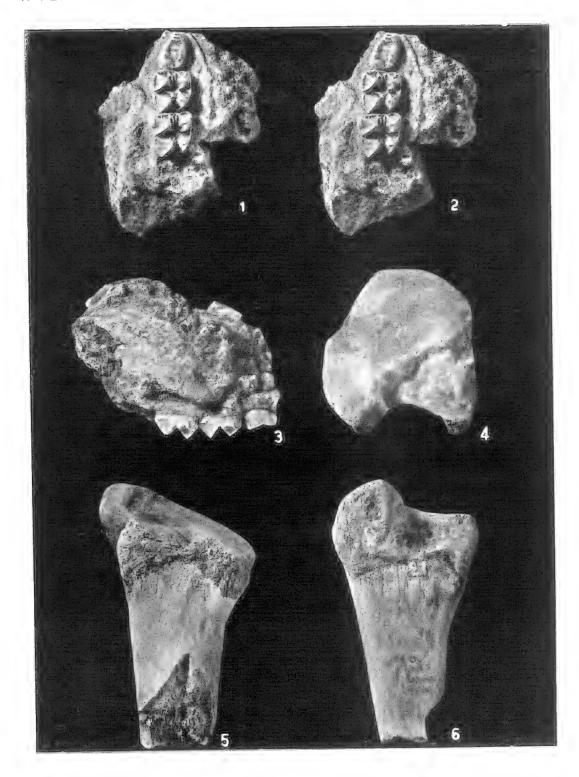
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PLATE 9

- Figs 1, 2: Stereopair of occlusal view, F5707, holotype, Phascolarctos stirtoni sp. nov.
- Fig. 3: Labial view of F5707, holotype, P. stirtoni sp. nov.
- Fig. 4: Distal view of F683, holotype, Koalemus ingens De Vis.
- Fig. 5: Posterior view of F683, holotype, K. ingens De Vis.
- Fig. 6: External view of F683, holotype, K. ingens De Vis.





AN ARCHAEOLOGICAL SITE SURVEY NEAR TAROOM, SOUTH-EASTERN QUEENSLAND

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The area chosen for this survey is part of the central highlands of Queensland. This district also includes the Carnarvon Gorge and Mt. Moffatt. Excavations have been undertaken at Cathedral Cave (Clegg, 1965) in the Carnarvon Gorge and, more importantly, those at the Tombs and Kenniff Cave near Mt. Moffatt (Mulvaney, 1965) have demonstrated human occupation of the region for at least sixteen thousand years. Other sites, particularly in the Carnarvon Gorge, are well known for paintings and engravings (Elkin, 1941; Goddard, 1941, 1942), which appear to belong to a distinct regional style, different from those recorded for northern New South Wales and for northern Queensland. This central highlands style is now recorded from the upper Dawson River valley towards the eastern limits of the region.

Since the country is extremely rugged it was not possible to examine the entire length of Robinson Creek as originally intended and only three small groups of sites (text-figure 1 Areas 2, 3, 4) were visited. The party was told of the existence of a number of other sites, notably in Mount Surprise National Park so that the survey cannot be considered exhaustive. However, certain interesting implications arise from the placement of the sites and their decoration. A small group of sites on the Dawson River near Robinson Creek (Area 1) was also investigated.

Site numbers quoted are Queensland Museum site survey reference numbers.

SITES EXAMINED

AREA 1. The sites are located near Postman Gully on the Dawson River. One (TAM 33) is a small cave close to the river bank, the other three (TAM 34, 35, and 36) are shelters. Two of these are in a small gully about two hundred yards from the north bank of the river; the third is a similar distance from the south bank up a small steep gully. All are decorated. In this area the Dawson River has permanent water and the country is open and rolling although the sandstone outcrops tend to erode into steep-sided gullies close to the river, thus forming many shelters and some caves.

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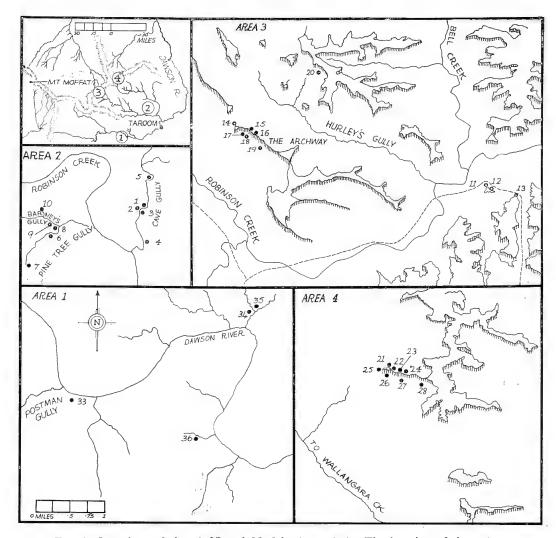


Fig. 1: Locations of sites 1-27 and 33-6 in Areas 1-4. The location of these Areas is shown in the upper left hand map.

AREA 2: Although it lacks permanent water, a similar description may be applied to the Cave Gully area on Robinson Creek, where an important group of sites (TAM 1–10) is located. Eight of these sites are decorated, one (TAM 3) is a find spot and one (TAM 5) appears to be a quarry and workshop. Five of the sites (TAM 1–5) are along Cave Gully on the north of the creek, the other five (TAM 6–10) are in the Pine Tree/Barney's/Blackfellers' Gully area to the south-west. In particular, site TAM 10 in Blackfellers' Gully, which is invisible from the surrounding plain, and where a large number of worked flakes were picked up from the surface, might repay detailed archaeological investigation.

AREA 3: The ten sites are divided between the head of Robinson Creek gorge (TAM 11, 12, and 13), the Archway (TAM 15–19), and the head of a small gully feeding to Bell Creek (TAM 20). Apart from an ochre source (TAM 19) all sites are decorated shelters. The situations of these shelters are rather different from those near Cave and Postman Gullies because of the different topography. This rugged upland region is an extremely dissected sandstone tableland, the remnants of which stand about three hundred feet above the valley floors. All the valley walls are steeply cliffed, the lower half being covered by talus slopes. The sites are located along the tops of these slopes and as a result they are always more than a quarter of a mile from the nearest water source. It is probably significant that all the sites recorded are clustered around prominent landmarks.

AREA 4: The terrain around the head waters of Wallangara Creek is equally as rugged as upper Robinson Creek. Of the eight sites recorded, one (TAM 28) is an ochre source, but the rest are decorated shelters. All these sites are located on a large bluff with a natural archway.

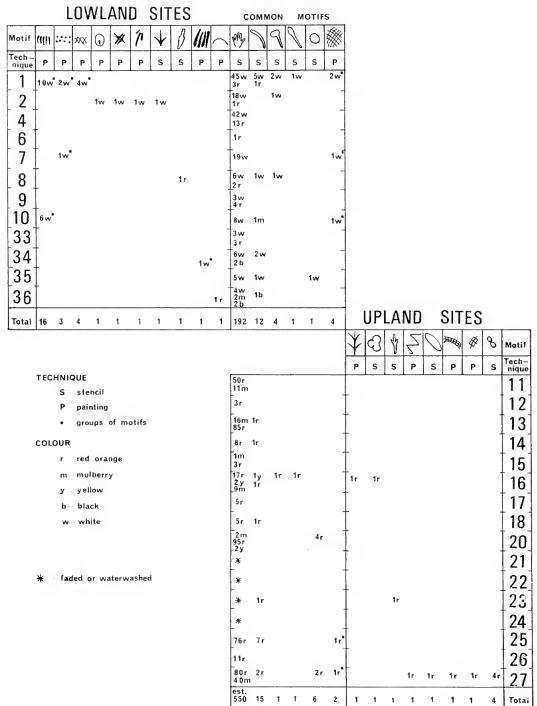
A number of contrasts may thus be drawn between upland and lowland sites. As well as those mentioned above some other differences are apparent. Of the twelve decorated sites in the lowland areas, six (TAM 1, 4, 6, 7, 10, and 33) are solution caves, low roofed, and semi-circular, having the front generally straight. These often appear to have only a small depth of deposit. The other six sites in Areas 1 and 2 are shelters. All these lowland sites are in sheltered and concealed places along the walls of gullies. In addition all lowland sites are within a quarter of a mile of water and close to resources of tool stone, particularly quartzite pebbles, and in general lowland sites are not intensively decorated, although TAM 4 and TAM 1 are exceptions.

The sixteen decorated upland sites are all shelters. Quite a variation in size was noted from the large sites (TAM 27, 20, 17, and 13) to the "cubby-hole" sized TAM 26. Seven of the sites are exposed to extensive water wash and flaking is common on the walls. None of the shelters is in as protected a position as the lowland ones, but even where water wash is worst, it is evident that the area decorated was formerly extensive and, as Table 1 shows, a very large number of paintings were recorded at many sites. No tool stone resources other than small quartz pebbles in the walls of some shelters were recorded near the upland sites.

PAINTINGS

Table 1 presents a summary of the numbers of paintings, colours, and techniques used in the twelve lowland (Areas 1 and 2) and sixteen upland decorated sites (Areas 3 and 4) which were examined.

 ${\bf TABLE~1} \\ {\bf Analysis~of~Paintings~According~to~Motif,~Technique,~Colour,~Numbers~and~Area.}$



It is important to note that no engravings and only two techniques of painting were recorded. These are the negative stencil (S on the table) and brushed on pigment (P). Both techniques occur in upland and lowland sites, although painted marks are more common in the latter. All paintings are monochromes.

The differences in colouration between lowland and upland sites are very striking. White and black never occur in the upland sites, yellow never in the lowland sites. Red-orange and mulberry colours are extremely rare in lowland sites, and it is interesting to note that in three sites (TAM 1, 9, and 10) red paintings are superimposed on white ones. White was never observed to be superimposed on red. A possible explanation for the red over white paintings is that the walls of the lowland shelters are generally blackened by fungus and present an unsuitable background for red pigments.

The majority of all paintings recorded in upland sites are a bright red-orange, but a deeper mulberry colour is also widespread. Yellow was recorded only at sites TAM 16 and 20. At site TAM 27, in Area 4, red-orange paintings were superimposed on mulberry ones and this raises the question of whether the mulberry-coloured pigment was originally red-orange. Rocks from the ochre sources TAM 19 and 28, which are mulberry-coloured in the hand specimens, give red-orange powders when freshly ground, but any direct evidence of colour change due to ageing is lacking. It should be added that the mulberry-coloured paintings appear to carry much less pigment than the red-orange ones. However, no transition of shade between bright red-orange and mulberry was noted, as might have been expected if the above suggestion was accepted, unless a long period of disuse separated paintings of the two colours.

Altogether 30 painting forms were recorded, and of these 20 occur uniquely. Six of these 20 forms can only be described as amorphous painted marks and are not listed in Table 1. Five such forms were recorded in upland sites and one in a lowland site. Of the ten repeated motifs, six are common to both types of country, while each of the other four occurs in but one area, and in two cases at one site only.

The six motifs common to both upland and lowland sites can be easily characterized. Four represent common tools—boomerangs, clubs, axes, and grinding stones, and are always stencilled. Boomerangs are usually shown horizontally, but one was pictured upright. Nulla nullas are also stencilled horizontally, as are axes, which are always shown with the blade down. More of the round marks interpreted as mullers (extreme left of plate 10, fig. 1) were recorded in upland sites. Here also the criss-cross pattern supposed to represent part of the *Macrozamia* palm (Goddard, 1941: 369–70) was found in very large patches, although the sign itself was also recorded in lowland sites where no stencilled mullers were seen.

Stencilled hands were by far the most common motif, accounting for 78 per cent of the lowland paintings and 93 per cent of the upland ones. They were seen in a great variety of forms and positions, particularly in upland sites. Here mainly left hands both large and small predominated, but hands and forearms both horizontal and vertical appeared, as did fists, hands with fingers bent under or mutilated, and hands in lateral view. Sites TAM 16 and 20 in Area 3 and site TAM 27 in Area 4 have extensive galleries of hands. Part of the gallery at this latter site is shown in plate 10, fig. 1.

Three of the motifs unique to site TAM 27 are shown in plate 10, fig. 2, while in contrast plate 10, fig. 3, is part of site TAM 1 in Area 2.

STONE TOOLS

Tool stone was collected where it appeared on the surface of the deposits. The materials included quartzite (74 per cent) chalcedonic silica (19 per cent), silicified wood (4 per cent) and quartz (3 per cent). Both quartz and quartzite occur in pebble form in the local sandstones, but chalcedonic silica and silicified wood appear to have been imported.

The collection totalled only 133 pieces, of which 83 per cent came from lowland sites. Collections were made at seven of the fourteen sites in Areas 1 and 2, but only three of the sixteen upland sites in Areas 3 and 4. As well, ochre samples were collected from the two upland sources. All surface tool stone material visible was collected, except at site TAM 5 in Cave Gully, which was an open workshop and quarry, and at the site in Blackfeller's Gully (TAM 10) where water scour at the front of the cave exposed large numbers of flakes and chips.

Whereas 53 per cent of the collection was used in some way, less than 3 per cent may be classified as formal tools (2 horsehoof cores and one "hand-axe"). These tools and two otherwise unused cores were found on lowland sites. Flakes make up 80 per cent of the whole collections, while chips and miscellaneous broken pieces account for 15 per cent.

The oval bifacially worked tool from TAM 5 in Cave Gully, shown in text-fig. 2a, is water-rolled, but closely resembles a rather crude hand-axe of the Euro-African tradition. A piece from TAM 10 in Blackfeller's Gully may be the tip of a similar tool (text-fig. 2b). A small horsehoof core from site TAM 33 on the Dawson River is also illustrated (text-fig. 2c).

A selection from the remaining 67 utilized pieces is shown in text-fig. 2d-n. Of these 55 are struck flakes which retain their striking platform, but otherwise show no consistent morphological pattern. An analysis of the 95 use fractured edges on these 67 pieces shows that 59 per cent are straight, 22 per cent are convex and 18 per cent are concave. Only 4 per cent of the utilized edges on these tools are retouched, and the used fractured edges vary from quite sharp to very blunt indicating a wide range of usage intensity.

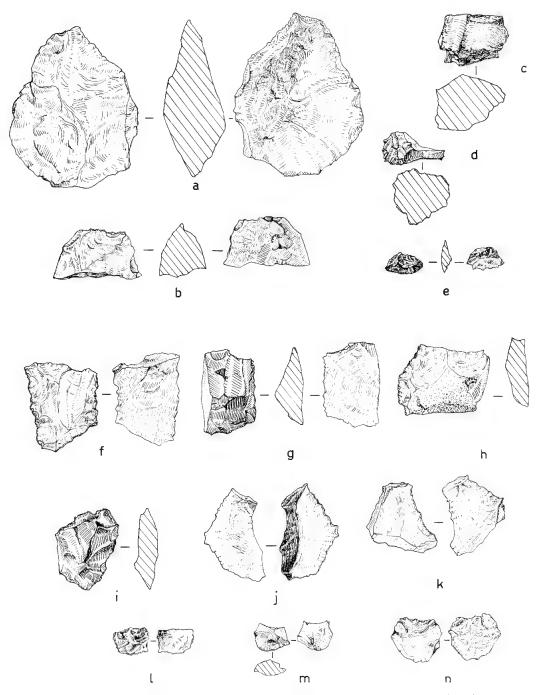


Fig. 2: A selection of the stone tools from sites in Areas 1-4. For explanation see text.

The twelve utilized pieces which do not seem to have come from struck flakes which retain a striking platform have a variety of forms and thicknesses. Those which do not appear to be broken struck flakes seem to have been the result of shatter, either deliberately by percussion or heating, or fortuitously.

The sizes and shapes of the utilized pieces tend to be less variable than those of the unutilized items. It was observed that the struck flakes tended to be long and narrow and that relatively more usage was found on the larger flakes.

DISCUSSION

Within the areas surveyed the striking differences in the situations of the sites and their decoration appear to be unusual for such a small part of one drainage system in Australia. How significant, then, are the contrasts drawn? All upland decorated sites are relatively unsheltered, landmark oriented, relatively far from water and tool stone sources, and exhibit extensive red paintings; whereas the lowland sites are in concealed and sheltered gullies, close to water and tool stone sources, and usually have minor decoration in white. The differences in painting colouration may have been due to the generally dark walls of the lowland sites and the pale ones of upland sites making ideal backgrounds for white and red respectively. While there is an emphasis on decoration in the upland sites, the large number of stone tools associated with the lowland sites suggest their predominance as manufacturing sites, no doubt due to their proximity to tool stone sources. The distance of the sites from water appears to be largely a function of topography, but the location of upland sites around easily recognizable landmarks must represent deliberate choice, for many suitable sites, particularly in Area 3, appear never to have been occupied.

Despite the important differences in painting colouration between Areas 1 and 2, and 3 and 4 of this survey, all paintings bear an obvious stylistic relationship to those found in the Carnarvon Gorge and Mount Moffatt areas. Motifs, techniques and colours in the upland sites in particular are similar to those in the Carnarvon Gorge as comparison of plate 10, figs 1 and 2, with Goddard (1941, plate 1c) shows. However, no single upland site in the Taroom district is as rich in paintings as the Art Gallery (Site SPE 8) in the Gorge (the 5 mile site, (Goddard, 1941:170)). Moreover, the engravings common in the Gorge sites (plate 10, fig. 4) were not found in the sites surveyed.

This extension of the area in which paintings typical of the Carnarvon Gorge occur is only to be expected, and the style may well extend over most of the central highlands. However the total distribution of this style and its relationships to the major painting styles of Australia are matters requiring further investigation.

ACKNOWLEDGEMENTS

The potential of the Robinson Creek district was first suggested to me by Mr. B. H. Ford of Miles, who organized preliminary contact with property holders in the area, without whose help the survey would have been impossible. I would particularly like to thank Mr. and Mrs. G. S. B. Jerrard of Robinson Creek, Mr. D. McConnell of Glenhaughton, and Mr. J. Hendricks of Yebna.

The survey was carried out with the assistance of Mr. A. J. Easton and Miss P. J. Wippell of the Queensland Museum staff.

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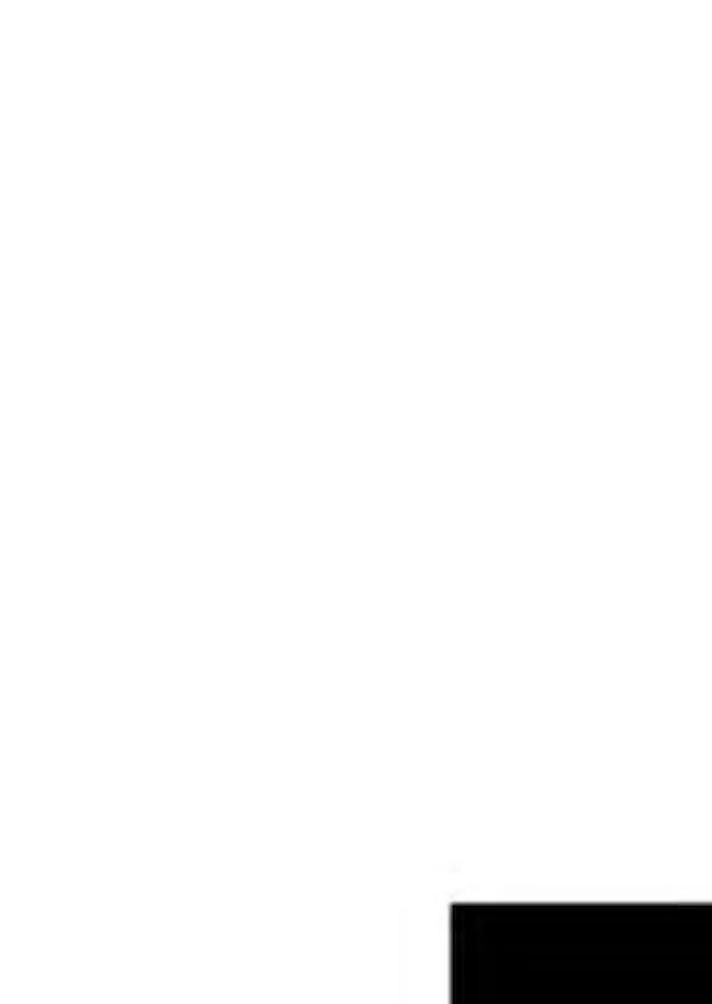
MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 10

Figs 1-3: Selected portions of the galleries at various sites. Figs 1, 2, TAM 27; fig. 3, TAM 1.

Fig.: 4: Some of the rock engravings at SPE 8, the Art Gallery in the Carnaryon National Park.





VARIABILITY IN THE SAND CRAB PORTUNUS PELAGICUS (LINNAEUS) (CRUSTACEA: PORTUNIDAE)

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SUMMARY

An unusual male of *P. pelagicus* is described. It differs from more typical specimens in twelve non-pigmentary, and four pigmentary features and in three of the latter resembles *P. trituberculatus*. There appears to be complete gradation to typical Queensland male specimens.

Differences in pigmentation between male *P. pelagicus* from different areas within its wide distributional range are commented upon.

Recent work to be published elsewhere (Stephenson in MS) involves detailed studies of pigmentation of large numbers of local sand crabs. Amongst the initial collections a single large male differed sufficiently in pigmentation and other features to be regarded tentatively as an undescribed species. While collection of additional material showed a gradation to typical forms, description of the extreme variant is considered necessary for four reasons:

- (1) to prevent the possible creation of an additional synonym by future workers,
- (2) to indicate an unexpected variability which has already had implications upon an attempt at numerical taxonomy (Stephenson, Williams and Lance 1968).
- (3) to focus attention on possible geographic variation in the species, which is commented upon in the Discussion, and
- (4) the specimen partly bridges the gap between *P. pelagicus* and *P. trituber-culatus* (Miers).

Throughout carapace breadths, measured by dial calipers, include the last anterolateral teeth, and are given to the nearest 1 mm.

All specimens have been deposited in the Queensland Museum.

DESCRIPTION OF UNUSUAL MALE (Fig. 1A, B, C; pl. 11A)

Male (c. 159 mm), trawled in shallow muddy grounds nr. St. Helena I., Moreton Bay by University Trawler "Wanderer II" (Mr. L. Wale), 15–25/viii/1966, Qd Mus. W. 2517.

EPISTOME: Stout projecting spine.

FRONT: With two rounded median lobes, and two sharp lateral teeth.

ORBITAL REGION: Inner orbital angle a sharp tooth. Upper border of orbit with deep but almost closed inner fissure, and open outer fissure. Region between these fissures almost bilobed. Suborbital fissure distinct. Suborbital border without hirsute margin (probably due to wear).

ANTEROLATERAL TEETH: First larger than those immediately after, remainder about equally sharp but increasing in basal width from second to eighth. Ninth very large and projecting straight out laterally.

CARAPACE: Very broad (B/L = $2\cdot15$), anterolateral borders forming broad arc with centre behind posterior border of carapace, postlateral junctions smoothly curved. Surface shining and granular except in postfrontal regions, bearing granular ridges, of which epibranchials are distinct, mesogastrics barely recognisable, and metagastrics are recognisable. Cardiac regions more densely granular than most of carapace, with granulation on the two sides almost confluent.

CHELIPEDS: (Left only present). Elongate, massive, spinous and ridged; under surface with faint corrugations. Under surface of arm terminating distally in stout rounded tubercle, upper surface with single posterodistal spine, and with five curved, sharp, stout anterior spines, the four distal being equally sized and spaced, and the proximal smaller and relatively close to its neighbour. Wrist with sharp outer and inner spines, the latter relatively short, both terminating carinae; three additional carinae on upper surface; anteroexternal border with rounded tubercle near its middle; angle between anteroexternal and anterointernal borders relatively obtuse. Upper surface of hand with stout spine at wrist articulation, and with three very conspicuous granular carinae:—(1) outer, separating upper from outer surface of hand, (2) subcentral, terminating in stout spine, and (3) inner, separating upper from inner surface of hand, also terminating in stout spine. Outer surface of hand

with acute, moderately finely granular central carina, and rounded feebly developed lower carina. Inner surface of hand with well-developed, smooth central carinae, terminating in spine. Fingers long, carinate and moderately strongly grooved with numerous rounded teeth.

WALKING LEGS: Inner margins of propodus and dactylus bearing thick fringe of hairs.

FIFTH LEG: With fringes of hairs on anterior edges of carpus, merus, and propodus, and to a lesser extent (? wear) on dactylus; also on posterior and posterodistal margins of propodus. No spines or spinules on posterior borders of segments.

THIRD MAXILLIPED: Anteroexternal angle of merus not produced laterally, upper surface of merus devoid of hairs. Anterior border with sparse hairs only (? wear).

MALE ABDOMEN: Gradually tapering, penultimate segment elongate but relatively broad basally, ultimate segment about as long as broad.

MALE FIRST PLEOPOD: As described by Stephenson and Campbell (1959) excepting that the arrangement of longer and stouter subterminal bristles roughly alternating with shorter and thinner bristles is less obvious.

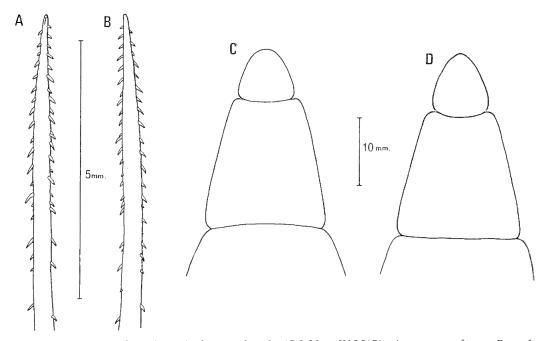


Fig. 1: A, B. Male first pleopod of unusual male (Qd Mus. W 2517); A, upper surface. B, under surface. C. Abdomen of above specimen. D. Abdomen of typical male (Qd Mus. W 2518).

COLOUR: After approximately four days in formalin predominantly dark purple red with lighter brownish purple in cardiac and mesobranchial portions of carapace.

Carapace: Somewhat sparsely mottled with pale blue areas outlined in dark brownish purple. The most conspicuous light marks are reniform spots in each post-lateral area with indistinct linear continuations towards cardiac region. Indistinct row of light spots behind frontal and anterolateral borders, terminating between sixth and seventh anterolateral teeth. Gastric and cardiac regions sparsely outlined with light blotches, becoming a conspicuous W mark in gastro-cardiac boundary. Small blotches near centre of epibranchial ridge. Near posterior border moderately dense mottling.

Chelipeds: Upper surface of arm with small white spots, sparsely arranged; anterior surface transversely divided into lilac upper distal half and ivory lower proximal half; lower surface ivory. Upper surface of wrist with numerous small white spots, outer surface with spots and patches of white, under surface white. Upper surface of hand between two inner carinae uniformly purple, between two outer carinae with two irregular lines of white spots; outer surface between two upper carinae with small white blotches on red purple background, and with pink and deep purple blotch at articulation of movable finger, lower portion white; inner surface between two upper carinae with numerous small white blotches on red purple background, and with conspicuous partly pink, partly deep purple, blotch at articulation of movable finger, lower portion cream bordered by blue-purple; under surface white externally and blue-purple with white spots internally. Finger predominantly blue-purple, without white mottling. Outer surfaces becoming pink towards the teeth and ivory towards articulation of movable finger.

Walking Legs: Upper surfaces of meri with small inconspicuous white spots.

Fifth Leg: Upper surfaces of merus and ischium with moderate numbers of white blotches.

DIFFERENCES FROM MORE TYPICAL LOCAL MALES (Fig. 1D; pl. 11B)

Comparisons are with similar sized specimens collected and preserved similarly (W2518 - W2523), with one specimen illustrated (W2518).

A. Non pigmentary features

- (1) Epistome stouter.
- (2) Median frontal lobes more rounded than in most P. pelagicus.
- (3) Orbit: upper border with inner fissure almost completely closed.
- (4) Cheliped arm: anterior border with five against typically four spines.
- (5) Cheliped wrist: inner spine relatively short.
- (6) Cheliped wrist; anteroexternal border with spine or spinule.
- (7) Cheliped wrist: angle between anteroexternal and anterointernal borders relatively obtuse.

- (8) Cheliped hand, outer surface: lower carina relatively feebly developed.
- (9) Cheliped hand, fingers: grooves only moderately well-developed.
- (10) Male abdomen: penultimate segment relatively broad basally.
- (11) Male abdomen: ultimate segment relatively short.
- (12) Male first pleopod, subterminal armature: two types of bristles less easy to distinguish.

B. Pigmentation

Comparison should be made between the description of the unusual specimen and that of typical males (e.g., Pl. 11B) which are as follows:—

After approximately fourteen days in formalin carapace predominantly light brownish purple with abundant lighter mottling, upper surface of appendages red purple with lighter mottling.

Carapace: Mottled with pale blue areas outlined in dark brownish purple. The most conspicuous light marks are reniform spots in each postlateral area continued as lines towards cardiac region. Distinct areas of spots and lines behind frontal and anterolateral borders, terminating between sixth and seventh anterolateral teeth. Gastric and cardiac regions clearly outlined with light blotches and lines, including a conspicuous W mark in gastro-cardiac boundary. Conspicuous light lines on inner portion epibranchial ridge, with further lines crossing borders of gastric region. Near lateral and posterior borders dense mottling.

Chelipeds: Upper surface of arm with fairly numerous white blotches, anterior surface indistinctly and transversely divided into blue upper distal half, and white lower proximal half, both halves with sparse dark blue spots. Upper and outer surfaces of wrist with large light blotches, under surface white. Upper surface of hand with moderate-sized light blotches and spots; outer surface between two upper carinae white with irregular purple meshwork and with pink and deep blue blotch at articulation of movable finger, lower portion white; inner surface between two upper carinae white with purple lines, between two lower carinae pale blue; under surface white externally and blue-purple with white spots internally. Fingers predominantly pink or white externally and pale blue internally, with upper proximal surface of movable finger with paler blotches.

Walking legs: Upper surfaces of meri with large white spots.

Fifth legs: Upper surfaces of merus and ischium densely blotched with white.

The most conspicuous colour differences of the unusual male are:

- (13) Darker background colour of carapace.
- (14) Reduced pattern of light markings on carapace.
- (15) Similar reduction on upper border of arm.
- (16) Sparser and larger light blotches on fifth leg.

INTERMEDIATE SPECIMENS

Material comprised: 4 males (W2513, 145 mm; W2514, 179 mm; W2515, 152 mm; W2516, c. 184 mm, soft specimen without chelae or walking legs), trawled near Mud I., Moreton Bay by University Trawler "Wanderer II" (Mr. L. Wale), 20/x/1966.

Referring to tabulated features A. (1) - (12), and B. (13) - (16) of the previous section, the resemblances of the above specimens to the original unusual one are:—

W2513: (3), (5), (9), ?(10), (11), (12), (13), (14), (15). i.e. about 9 out of 16 features.

W2514: (1), (2), ?(4)*, (5), (7), (8), (9), (11), (12), ?(15)*. i.e. about 9 out of 16 features.

W2515: (2), (6), (8), ?(12). i.e. about 4 out of 16 features.

W2516: (1), (2), (3), (10), (11), (13), (14). i.e. about 7 out of $9\dagger$ features.

It is evident that there is considerable gradation from unusual to usual specimens, and that there is no combination of features whereby the unusual specimens can be segregated.

DISCUSSION

The existence of an almost continuous variation in local specimens of male *P. pelagicus* from an extreme form to "normal" has been demonstrated. Many (but not all) of the differences between the extreme and normal forms concern pigmentation, and presumably this is genetically determined, because specimens were of similar sizes, caught by similar techniques, all essentially in the same area. In some respects (e.g. features (13), (14) and (16)) colouration of the unusual specimens resembles that of *P. trituberculatus* (Miers) as figured by Sakai, 1939 (pl. 50) and particularly by Sakai, 1965 (pl. 54). There are, however still numerous colour differences as compared with *P. trituberculatus*.

In the closely related *P. sanguinolentus* (Herbst), the present author has shown that there are geographically distinct groups with noticeably different pigmentation, which probably have the status of subspecies. Comparison of males of *P. pelagicus* from Japan and Queensland has been effected through the loan of Japanese specimens by Dr. Yatsuzuka (figured by Stephenson in MS), and by comparison with Sakai's plates. These suggest that geographical differences occur in the pigmentation of male specimens of *P. pelagicus* as well as in *P. sanguinolentus*. Thus in Queensland specimens the central gastric light mark of Japanese specimens is absent or barely recognisable, while the postlateral and posterior portions of the carapace are noticeably more ocellated.

^{*} In W2514, features (4) and (15) agreed with the unusual specimen in the left cheliped, but not in the right.

[†] Only nine features visible on this incomplete specimen.

The figure and description given of *P. pelagicus* by Crosnier (1962, pp. 43–5, text-fig. 58) suggest yet another detailed type of patterning in Madagascar specimens, which possess in Crosnier's words (p. 45) "Nombreuses vermiculations claires". This has been confirmed by the examination of a recently preserved Madgascar male (123 mm) kindly provided by Dr. Crosnier. The patterning throughout shows many more pale rounded or polygonal areas on the carapace than in typical Queensland specimens, this applies particularly to the anterior mesobranchial and cardiac regions. The reniform spot in each postlateral area, while visible, has a much less obvious linear continuation towards the cardiac region.

In addition the ultimate segment of the male abdomen of Crosnier's specimen differs slightly from those of the Queensland specimens, somewhat resembling that of fig. 1D, but broader basally. Crosnier's figures of the first pleopod of a Madagascar specimen also differ slightly from those of Queensland material.

It is evident that it would be of considerable interest at the subspecific level to examine large numbers of specimens of *P. pelagicus* at different points within the Indo-West Pacific range of the species.

ACKNOWLEDGMENTS

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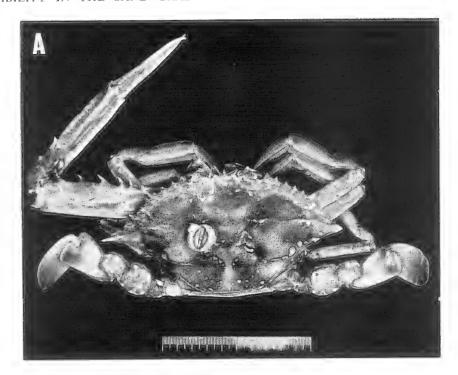
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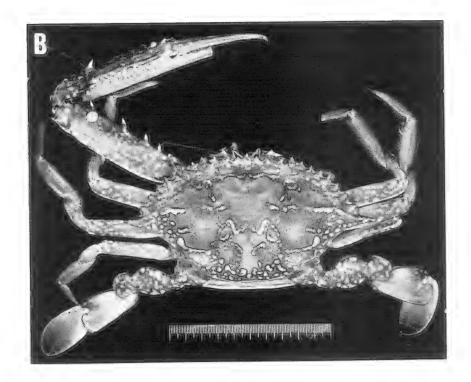
MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 11

Portunus pelagicus. Dorsal views showing variation in pigment.

- A. Unusual male, Qd Mus. W 2517.
- B. Typical male, Qd Mus. W 2518.







A REVISION OF THE *CHARYBDIS MILES* "GROUP" OF SPECIES (CRUSTACEA: PORTUNIDAE), WITH DESCRIPTION OF A NEW SPECIES FROM OUEENSLAND WATERS

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A dried specimen of *Charybdis*, which had been collected from fairly deep waters off southern Queensland, proved to be close to, but distinct from, *C. riversandersoni* Alcock. It is here described as *C. rufodactylus* n. sp. As already noted by Stephenson and Rees (1967) and by Stephenson (1967), *C. riversandersoni* and *C. miles* (de Haan) resemble each other more closely than might be expected from Leene's (1938) monograph, and the discovery of the new species gave sufficient homogeneity to the three species for them to be regarded as a closely related "group".

In comparing similarities and differences between the three species it became evident that *C. riversandersoni* in particular showed unexpected variability, and additional material was variously borrowed. This revealed that part of the variation was due to confusion between *C. riversandersoni* and *C. sagamiensis* Parisi, and that the latter species, which had been synonymised with the former, merits independent status.

Because of the difficulties in identifying species in this group, past records which omit structural features may have been referred to the wrong species. In cases where confirmation was not obtained by examination of specimens, such records are indicated in the synonymy by:—"(record only)".

Dimensions were measured by dial calipers to the nearest 0.1 mm. Breadths of specimens include the last anterolateral teeth, and are given only to the nearest 0.5 mm. Carapace lengths were measured in the midline from the base of the notch between the median frontal teeth to the centre of the posterior margin of the carapace. Breadth/length ratios of carapaces varied, and this variation appeared to be mostly at an individual level, rather than being size dependent. Only mean breadth/length ratios of carapace are given.

Breadths of fifth legs were measured in the widest portions proximal to the posterolateral spines. Length/breadth ratios were shown to vary with the species, and also with the size of the specimen, and hence in the specific descriptions there is a deliberate lack of precision. The relevant data are given in fig. 3.

Charybdis miles (de Haan)

(Figs. 1A, 1E, 2A; pl. 12A)

- Portunus (Charybdis) miles de Haan, 1835, p. 41, pl. 11, fig. 1.
- Charybdis miles (de Haan). Stimpson, 1858, p. 39. Whitelegge, 1900, p. 157. Doflein, 1902, p. 659. Rathbun, 1902, p. 27. Stimpson, 1907, p. 82. Parisi, 1916, p. 175.
 Balss, 1922, p. 104. Yokoya, 1933, p. 195 (record only). Sakai, 1934, p. 302; 1936, p. 123, pl. 33, fig. 2; 1939, p. 405, pl. 46, fig. 2; 1965, p. 123, pl. 61. Stephenson, 1967.
 p. 11. Stephenson and Rees, 1967b, p. 6.
- Goniosoma miles (de Haan). A. Milne Edwards, 1861, pp. 378, 385. Ortmann, 1893, p. 81 (record only).
- Charybdis (Goniosoma) miles (de Haan). Alcock, 1899, pp. 62-3. Chopra, 1935, p. 485, fig. 9. Shen, 1937, p. 123, fig. 13.
- Charybdis (Gonioneptunus) investigatoris Alcock, 1899, p. 70. Alcock and Anderson, 1900, pl. 46, fig. 4.
- Charybdis (Charybdis) miles (de Haan). Leene, 1938, pp. 38-43, figs. 10-13. Stephenson, Hudson and Campbell, 1957, pp. 500-1, figs. 2H, 3I, pl. 2, fig. 3, pl. 4F. Rees and Stephenson, 1966, p. 37. Stephenson and Rees, 1967a, p. 11.

MATERIAL EXAMINED

From Queensland Museum, Brisbane: Male (54 mm), Arnhem Bay, N. Territory, 10 fm, sand and mud bottoms, coll. V. Wells, W2431; male (83 mm*), female (59.5 mm) trawled 40 miles N. of Cape Moreton, Qd, 62 fm, coll. Zool. Dept Univ. Qd, 10/viii/1966, W2784.

From Dr. T. Sakai: 4 females, Sagami Bay, 30-50 m, Qd Mus. W 2783.

From Australian Museum, Sydney: 7 males (36·5-60 mm), 3 females (38·5-57 mm), "Thetis" Stas. 21, 24, 25, Newcastle Bight, N.S. Wales, 28-40 fm, E. R. Waite, G2170, G2210, G2355; 4 males (37-66 mm), female (46 mm), "Thetis" Sta. 22, Newcastle Bight, N.S. Wales, 26-40 fm, E. R. Waite, G2352; female (64 mm), off Botany Bay, N.S. Wales, deep water, from deck and nets of trawler "Thistle", pres. M. Ward, Oct., 1924, P7870. Male (38·5 mm), Stockton Bight, N.S. Wales, 75 fm, trawled in association with prawns, A. A. Racek, Feb. 1960, P14188; ovig. female (69 mm), "Kestrel" Sta. 6, Southern Gulf of Carpentaria, Qd, C.S.I.R.O. Prawn Survey, 1963-64, P14847; male (51·5 mm), trawled 13 miles off Clarence River mouth, N.S. Wales, 34-40 fm, F. Ellen, March 1965, P15167.

From Smithsonian Oceanographic Sorting Centre, International Indian Ocean Expedition Collections: Male (52 mm), ovig. female (47·5 mm), "Anton Bruun" Cr. 1, Sta. AB–20, 09° 13′ N., 95° 51′ E., trawled, 60–58 m, 23/iii/1963; male (51·5 mm), "Anton Bruun" Cr. 1, Sta. AB21–63, 09° 54′ N., 97° 42′ E., trawled, 70 m, 24/iii/1963; male (26·5 mm), female (28 mm), "Anton Bruun" Cr. 4B, Sta. 255A, 25° 50′ N., 57° 07′ E. – 25° 45′ N., 57° 07′ E., trawled 92 – 95 m, clay, mud, sand, minute gastropod shells, 30/xi/1963; 4 males (21·5–54 mm), ovig. female (47·5 mm), "Anton Bruun" Cr. 4B, Sta. 256A, 26° 10′ N., 57° 02′ E. – 26° 13′ N., 57° 02′ E., trawled. 64–55 m, green mud, 30/xi/1963; female (54·5 mm), "Anton Bruun" Cr. 4B, Sta. 261A, 25° 52′ N.,

56° 53′ E. – 25° 53′ N., 56° 53′ E., trawled, 99 m, green mud with few small shells, 1/xii/1963; male (81·5 mm†), female (30·5 mm), "Anton Bruun" Cr. 4B, Sta. 262A, 25° 37′ N., 56° 34′ E. – 25° 39′ N., 56° 34′ E., trawled, 79 m, green muddy sand, 1/xii/1963.

From Smithsonian Institution, U.S.N.M.: Male (84 mm), Dale, Palos, Bore I., received 19/xii/1881 (Japan), 5259; 2 males (58·5, 84·5 mm), ovig. female (51 mm), Wakanoura, Kii, Japan, Jordan and Snyder, Stanford University 1900, 26261; male (55 mm), Tomaga Shima Lt. bet. Kobe and Yokohama, Sta. 4964, 37 fm, 27/viii/1906, 50794; male (31·5 mm), Mogi, Japan, exch. Imperial University, Tokyo, 45855; male (74 mm), China, S. F. Light, 61977; ovig. female (61·5 mm), San Andreas I. bet. Marinduque and Luzon, Sta. 5220, 50 fm, 24/iv/1908, Albatross Philippine Exped., 50792; juv. female (21·5 mm), San Fernando Pt., W. coast Luzon, P.I., Sta. 5442, 45 fm, coarse sand, 16° 30′ 36″ N., 120° 11′ 06″ E., 11/v/1909, Albatross Philippine Exped., 112310 (rounded frontal teeth).

From Scripps Institution of Oceanography: 2 males (54·5, 60 mm), "Naga" Sta. 59–0052, Gulf of Siam, 08° 40′ N., 102° 18·5′ E., 70 m, trawled, 24/x/1959, Cat. No. 43–0144; female (56·5 mm), "Naga" Sta. 60–0212, S. China Sea, 15° 40′ N., 109° 22·9′ E., 60–108 fm, trawled, 27/ii/1960, Cat. No. 43–00115; male (22·5 mm), Sacculina infected specimen (27 mm), "Naga" Sta. 60–0237, Hon Lon, Viet Nam, 12° 09·7′ N., 109° 24·7′ E., 91–101 m, trawled, 4/iii/1960, Cat. No. 43–00129; male (53 mm), "Naga" Sta. 60–0636, Gulf of Siam, 10° 19·8′ N., 102° 25·8′ E., 62 m, trawled, 7/viii/1960, Cat. No. 43–00147; female (48 mm), "Naga" Sta. 60–0777, S. China Sea, 12° 09·7′ N., 109° 24′ E., 93 m, trawled, 20/ix/1960, Cat. No. 43–00150.

From Zoologisch Museum, Amsterdam: Ovig. female (65.5 mm), "Siboga" Sta. 318, 06° 36.5' N., 114° 55.5' E., 88 m.

From British Museum: Male (87.5 mm), Tosa Bay, Japan, K. Sakai, 1961, 6.5.63; male (48 mm), female (46.5 mm), Tanabe Bay, Japan, Mr. Yamamato, Seto Marine Lab., 1961, 11.13. 39/40; male (67 mm), Hong Kong, Barney, 1930, 12.2.102 (prev. ident. by J. E. Leene); 2 females (47.5, 52.5 mm), Newcastle Bight, N.S. Wales, Australia, 28–40 fms., pres. Australian Museum, 1912, 11.22.66/67 (prev. ident. by T. Whitelegge).

MATERIAL ILLUSTRATED

Figs. 1A, 2A, specimen † above. Pl. 12A, specimen * above.

DESCRIPTION

FRONT: Six toothed, with medians and submedians relatively stout and acutely or roundedly triangular, and laterals narrow and acute. Medians separated by relatively shallow fissure, pointing directly forwards. Submedians separated from medians by broad shallow fissure, inclined laterally particularly inner borders. Laterals, separated from submedians by moderately wide fissure, directed forwards. Inner supraorbital angles moderately sharp but stout, inner supraorbital fissure widely open, outer fissure barely open. General suborbital border granular. Suborbital fissure very wide and deep.

Anterolateral Teeth: Six; first relatively short with truncate sometimes almost bifid margin; second to fifth broad-based, sharp-tipped, with anterior borders concave, and with third and fourth slightly larger than second and fifth. Sixth relatively short, directed somewhat forwards and slightly upwards.

CARAPACE: Relatively narrow (mean B/L 1·44), with fine pile through which well-developed granular ridges visible, beneath pile some granular patches. Posterolateral borders long and very little inclined. Postlateral junction rounded. Branchial regions at most very slightly swollen. Granular ridges as follows: frontal just recognisable; protogastrics of moderate length, widely separated, almost straight; mesogastrics almost straight; metagastrics narrowly separated in midline and almost straight; epibranchials conspicuous, moderately curved. Fine diffuse granular patches as follows visible after removal of pile: on bases of frontal teeth; sometimes small patches behind frontal ridges; between protogastrics and mesogastrics; on mesobranchial regions; on bases of first to fifth anterolateral teeth. Posterior part of cervical grooves fairly widely separated, moderately distant from metagastric ridges.

CHELIPEDS: Long, spinous, upper surfaces densely hirsute, hand slightly swollen. Arm with anterior border bearing 3–5 spines which are curved, sharp and either slender or robust; upper surface mostly fairly coarsely granular; under surface granular on projecting pertion, terminating in boss with spine or tubercle. Wrist with inner and three outer spines; inner spine long; carinae running to inner spine and to upper and lower of three outer spines. Upper surface of hand with four sharp spines including one at wrist articulation, one near centre of outer margin, and two on inner margin (one roughly at middle, one on distal border); outer surface with central carina very well-developed and composed of fused granules, above this well-developed squamiform markings, these sometimes also below carina; under surface strongly squamiform; inner surface with strongly developed central carina with conspicuous squamiform markings on areas above and below carina. Movable finger long, slender and deeply grooved. Immovable finger with inner and outer surfaces as movable finger; under surface deeply grooved.

WALKING LEGS: Moderately long and slender, for example carpus of last walking leg moderately elongate and narrow.

FIFTH LEG: Merus fairly broad (see fig. 3); spine on posterodistal border. Propodus with 0-5 typically 2 spinules on posterodistal border.

MALE ABDOMEN: Penultimate segment broader than long. Ultimate segment of moderate length.

MALE FIRST PLEOPOD: Sinuous, without obvious membrane. Subterminal armature: inner side, short bristles to aperture; outer side, relatively short row of long bristles, with concentration just behind tip, thereafter sparse.

PIGMENTATION (recently preserved specimens): Features common to all four species are separately listed (see p. 106). Distinctive features are:—movable finger, upper and inner surface, proximal half pale pink and white, distal half pink; outer surface cream becoming pale pink near tip, or with mottled or barred pink and white.

Immovable finger, outer surface, proximal half to two-thirds cream or pink, remainder pale pink to red, this extending backwards almost to level of articulation of movable finger; inner surface, proximal one-third to half mostly cream with pink or red distal area.

COMMENTS

This species differs considerably from the remainder, and possesses the following distinctive features apart from pigmentation:

- (1) Median frontal teeth separated by relatively shallow fissure.
- (2) Suborbital fissure very wide and deep.
- (3) Sixth anterolateral tooth relatively short.
- (4) Carapace relatively narrow, with fine pile.
- (5) Upper surfaces of chelipeds densely hirsute.
- (6) Hand of cheliped with under surface strongly squamiform, and squamiform markings on inner surface above and below central carina.
- (7) Immovable finger with under surface deeply grooved.
- (8) Fifth leg with relatively broad merus.
- (9) Male first pleopod, subterminal armature on outer side with relatively short row of long bristles with concentration behind tip.

Distribution is from the Gulf of Oman, India, Singapore, and Japan, to the Philippines and Australia.

Charybdis riversandersoni Alcock

(Figs. 1B, 1F, 2B, 2D; pl. 12B)

Charybdis (Goniosoma) riversandersoni Alcock, 1899, p. 53. Alcock and McArdle, 1902, pl. 40, fig. 3. Gordon, 1931, p. 538, fig. 13c (under C. (G.) barneyi).

Charybdis (Charybdis) riversandersoni Alcock. Leene, 1938, pp. 28-30, figs. 3, 4a, 4b.

Charybdis riversandersoni Alcock. Stephenson, 1967, p. 12. Stephenson and Rees, 1967b; pp. 7–8.

[non] Charybdis riversandersoni Alcock. Balss, 1922, p. 105. Sakai, 1939, pp. 404–5, pl. 46, fig. 1; 1965, pp. 122–3, pl. 60, fig. 2. (= C. sagamiensis Parisi).

MATERIAL EXAMINED

From Smithsonian Oceanographic Sorting Center, International Indian Ocean Expedition Collections: Female (26 mm), "Anton Bruun" Cr. 4B, Sta. 202 A, 17° 25′ N., 71° 39′ E. – 17° 21′ N., 71° 41′ E., trawled, 96–106 m, greenish sand and mud, 13/xi/1963. 2 males (65·5†, 75·5* mm), "Anton Bruun", Cr. 4B, Sta. 263 A, 25° 12′ N., 56° 47′ E. – 25° 12′ N., 56° 51′ E., trawled, 206 m, grey soft mud, 2/xii/1963. Male (18·5 mm), 2 females (26, 34·5 mm), one extra cheliped, "Anton Bruun" Cr. 4B, Sta. 264 A, 25° 02′ N., 56° 52′ E. – 25° 08′ N., 56° 52′ E., trawled, 291–272 m, sticky grey clay and mud, 2/xii/1963.

From Scripps Institution: Male (67 mm), damaged female (42·5 mm), "Naga" Sta. 60–0212, S. China Sea, 15° 40′ N., 109° 22·9′ E., 60–108 fm, trawled, 27/ii/1960, Cat. No. 43–00116.

From British Museum: Male (61.5 mm), 7° 27' N., 71° 41' E., pres. Indian Museum, 99:8:26:2.

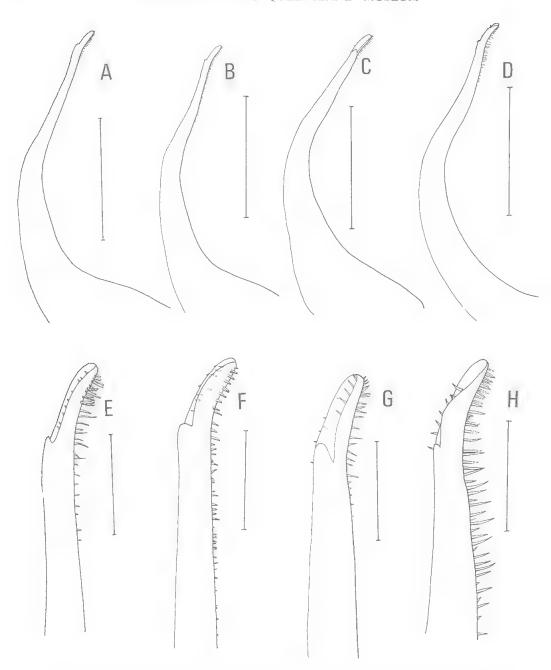


Fig. 1: Male first pleopods, upper view, A-D whole pleopods (scale 5 mm), E-H tips of pleopods (scale 1 mm). A, Charybdis miles; B, C. riversandersoni; C, C. sagamiensis; D, C. rufodactylus; E, C. miles; F, C. riversandersoni; G, C. sagamiensis; H, C. rufodactylus.

MATERIAL ILLUSTRATED

Pl. 12B and Figs. 1B, 1F and 2B, specimen * above. Fig. 2D, specimen † above.

DESCRIPTION

FRONT: Six toothed, with medians and submedians relatively stout, laterals narrow, elongate and acute. Medians separated by moderately deep fissure, roundedly triangular, pointing directly forwards and slightly narrower than submedians. Submedians separated from medians by relatively broad fissure, triangular with pointed tips, and inclined laterally. Laterals separated from submedians by moderately wide fissure, pointing directly forwards or inclined a little medianly. Inner supraorbital angles moderately sharp but stout. Inner supraorbital fissure widely open; outer fissure barely open. General suborbital border granular. Suborbital fissure wide.

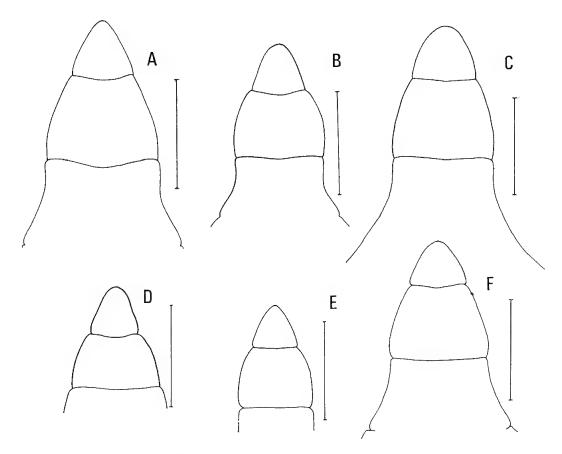


FIG. 2: Male abdomens (scale 10 mm). A, C. miles; B, C. riversandersoni; C, C. sagamiensis; D, C. riversandersoni; E, C. sagamiensis; F, C. rufodactylus.

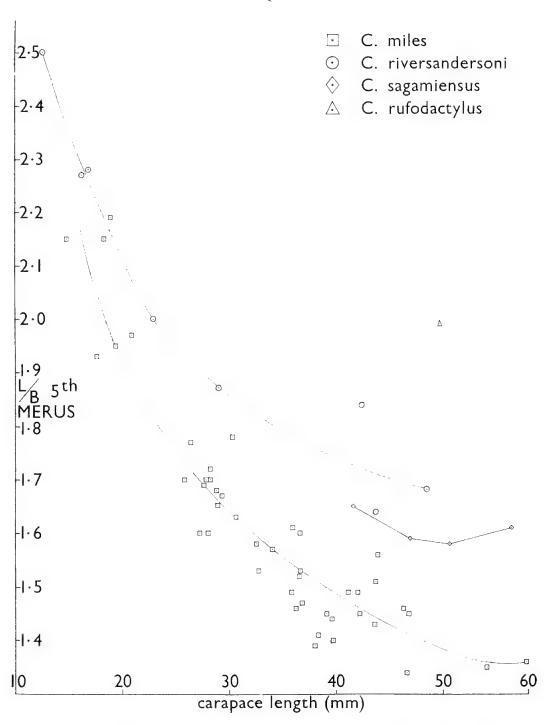


Fig. 3: L/B ratios of merus of fifth leg plotted against carapace length. Each point represents a single individual, and when two meri are present the L/B ratio is the mean. Curves through the C. miles and the C. riversandersoni data have been smoothed visually.

ANTEROLATERAL TEETH: Six; first short and narrow with truncate margin; second to fifth broad-based, sharp-tipped, with anterior borders concave, and with second relatively short particularly its tip, third and fourth relatively broad, fifth relatively sharp and protruding. Sixth sharp, of moderate length and directed laterally and a little upwards.

CARAPACE: Relatively broad (mean B/L 1·54), without hairs, feebly developed granular ridges, granular patches not present. Posterolateral borders short and much inclined. Postlateral junction rounded. Branchial regions swollen. Finely granular ridges as follows: protogastrics short, very widely separated, slightly convex anteriorly; mesogastrics almost straight; metagastrics very widely separated in midline and barely recognisable; epibranchials fairly conspicuous, moderately curved. Posterior part of cervical grooves deep, narrowly separated, distant from metagastric ridges.

CHELIPEDS: Long, spinous, upper surfaces smooth, hand swollen. Arm with anterior border bearing 3–4 spines (four in larger specimens) which are curved, sharp, and either slender or robust; upper and under surfaces smooth and polished; under surface terminating distally in boss with tubercle or spine. Wrist with inner and three outer spines; inner spine short and stout; obscure carina running to inner spine, carinae running to upper and lower of the three outer spines. Hand with four short, robust spines, including one at wrist articulation, one near centre of outer margin, and two on inner margin, one roughly at middle, one on distal border; outer surface with central carina a low rounded ridge, above this faint squamiform markings; under surface smooth; inner surface with carina a rounded ridge often indistinct proximally, above and below carina smooth. Movable finger long, slender, moderately deeply grooved. Immovable finger with inner and outer surfaces as movable finger; under surface smooth and rounded.

WALKING LEGS: Moderately slender, for example carpus of last walking leg relatively elongate.

FIFTH LEG: Merus elongate (see fig. 3); spine on posterodistal border. Propodus with 0–4 spinules on posterodistal border.

MALE ABDOMEN: Penultimate segment broader than long, sometimes slightly so, sometimes very much so. Ultimate segment relatively elongate.

MALE FIRST PLEOPOD: Sinuous, without obvious membrane. Subterminal armature: inner side, short bristles to aperture; outer side, elongate row of moderately short bristles.

PIGMENTATION (recently preserved specimens): Features common to all four species are separately listed (see p. 106). Distinctive features are:—movable finger, upper and inner surfaces, proximal half cream, distal half pink; outer surface, distal half to two-thirds cream, remainder pale pink. Immovable finger, outer surface, proximal two-thirds cream, distal one-third pale pink, pigment extending backwards on under surface but not to level of articulation of movable finger; inner surface, proximal one-third to half entirely cream with sharp oblique separation from pink distal area.

COMMENTS

This species is close to *C. sagamiensis* and the resemblances are detailed in the Discussion. Distribution is Gulf of Oman, East Coast of India, and South China Sea.

Charybdis sagamiensis Parisi

(Figs. 1C, 1G, 2C, 2E; pl. 12C)

Charybdis sagamiensis Parisi, 1916, p. 175, pl. 11, fig. 1.

Charybdis riversandersoni Alcock. Balss, 1922, p. 105. Sakai, 1939, pp. 404-5, pl. 46, fig. 1; 1965, pp. 122-3, pl. 60, fig. 2.

[non] Charybdis (Goniosoma) riversandersoni Alcock.

MATERIAL EXAMINED

From Dr. T. Sakai: Male (61.5 mm)†, female (73.5 mm), coast of Mikawa, central Japan, 30-50 m., † Qd Mus., W2785.

From Museum National d'Histoire Naturelle, Paris: Male (78 mm)*, Japon, Frank (? ifs), 1895; male (85·5 mm), Viet Nam, Campagne du "de Sanessa", don. Mr. Krempf, 1925–1926.

From British Museum: 2 females (35·5, 41 mm), Tosa Bay, Japan, K. Sakai, 1961, 6.5.61/62. The following specimen may belong to the above species.

From Smithsonian Institution, U.S.N.M.: Male (62.5 mm), Misaki, Japan, A. S. Pearse (don.), brought from Kuma-san, 1930, 63679 (prev. ident. M. J. Rathbun as C. miles).

MATERIAL ILLUSTRATED

Pl. 12C and Figs. 1C, 1G and 2C, specimen * above; Fig. 2E, specimen † above.

DESCRIPTION

FRONT: Six toothed, with medians and submedians relatively stout and triangular (apparently sharp-tipped when undamaged), laterals narrow, elongate and acute. Medians separated by deep fissure, pointing directly forwards and slightly narrower than submedians. Submedians separated from medians by moderately deep fissure, inclined slightly laterally, mostly their inner borders. Laterals separated from submedians by relatively deep fissure, pointing directly forwards. Inner supraorbital angles sharp. Inner supraorbital fissure narrowly open, outer fissure barely open. General suborbital border granular. Suborbital fissure wide.

ANTEROLATERAL TEETH: Six; first relatively short with truncate or almost bifid margin; second to fifth broad-based, sharp-tipped with anterior borders distinctly concave and with third and fourth slightly larger than second and fifth. Sixth sharp, relatively long, curved forwards and upwards.

CARAPACE: Relatively broad (mean B/L 1·53), without hairs, with well developed granular ridges, general surface with fine diffuse granular patches. Posterolateral borders short and much inclined. Postlateral junction rounded. Branchial regions at most faintly swollen. Granular ridges as follows: protogastrics fairly short, very widely separated, slightly convex anteriorly; mesogastrics almost straight; metagastrics moderately separated in midline, almost straight; epibranchials conspicuous, curved. Fine diffuse granular patches on unworn specimens as follows: on bases of frontal teeth; between protogastrics and mesogastrics; just behind inner terminations of epibranchial ridges; very fine granules on bases of first to fifth anterolateral teeth. Posterior part of cervical grooves moderately deep, fairly widely separated, distant from metagastric ridges.

CHELIPEDS: Massive, spinous, upper surfaces mostly hairless, hand swollen. Arm with anterior border bearing 3–4 spines which are curved, sharp and robust; upper surface mostly very finely granular; under surface smooth, terminating in boss with spine or tubercle. Wrist with inner and three outer spines, inner spine of moderate length and sharp; carinae running to inner spine and to upper and lower of three outer spines. Upper surface of hand with four sharp, stout spines including one at wrist articulation, one near centre of outer margin, and two on inner margin, one roughly at middle, one on distal border; outer surface with central carina a rounded ridge, above this recognisable squamiform markings; under surface with hint of squamiform markings; inner surface with central carina a rounded ridge, above and below carina smooth. Movable finger relatively short and stout, moderately deeply grooved in smaller specimens and shallower grooves in larger specimens. Immovable finger with inner and outer surfaces as movable finger; under surface smooth and rounded.

WALKING LEGS: Moderately robust, for example carpus of last walking leg relatively short and broad.

FIFTH LEG: Merus of moderate length (see fig. 3); spine on posterodistal border. Propodus with 0–2, typically 2, spinules on posterodistal border.

MALE ABDOMEN: Penultimate segment of variable width and always broader than long. Ultimate segment of moderate length.

MALE FIRST PLEOPOD: Sinuous, without obvious membrane. Subterminal armature: inner side, bristles to aperture, sometimes inconspicuous in profile view; outer side, concentration of bristles behind tip thereafter sparse row of variable length, short (1 specimen) or long (2 specimens).

PIGMENTATION (recently preserved specimens): Features common to all four species are separately listed (see p. 106). Distinctive features are: movable finger, upper, inner and outer surfaces, proximal half pale pink and white, distal half red. Immovable finger, outer surface, proximal half pale pink, sharply demarcated from distal half red, no backwards extension of red pigment in side view; inner surface, proximal one-third to half mostly cream with oblique separation from pink distal area.

COMMENTS

This species is close to *C. riversandersoni* and the resemblances are detailed in the Discussion. Distribution is Viet Nam to Japan.

Charybdis rufodactylus n. sp. (Figs. 1D, 1H, 2F; pl. 12D)

MATERIAL EXAMINED AND ILLUSTRATED

Holotype: Male (75·5 mm), (dried), trawled 100 fm off Cape Moreton, southern Queensland, L. Wale, June 1964, don. Zool. Dept Univ. Qd, Qd Mus. W2573.

DESCRIPTION

FRONT: Six very acute, pointed teeth. Medians broader than submedians and separated by deep angular fissure, pointing slightly outwards; submedians separated from medians by broad, deep fissure, inclined slightly outwards, particularly their inner borders which are concave. Wide and deep incision between submedians and laterals which are long, thin and inclined directly forwards. Inner supraorbital angles sharp and acutely pointed. Inner supraorbital fissure narrowly open; outer fissure barely open. General suborbital border granular. Suborbital fissure wide.

Anterolateral Teeth: Six, first relatively short with almost bifid margin; second to fifth broad-based, very sharp-tipped with anterior borders distinctly concave, becoming sharper and more slender from second to fifth. Sixth sharp, relatively long, directed outwards and slightly upwards.

CARAPACE: Relatively broad (B/L 1·51), with fine pile visible in postlateral portions, with well-developed granular ridges, also with granular areas. Posterolateral borders short and much inclined. Postlateral junction rounded. Branchial regions at most faintly swollen. Granular ridges as follows: frontals short but conspicuous; protogastrics fairly short, widely separated, convex anteriorly; mesogastrics sinuous, bow-shaped; metagastrics with fairly narrow separation in midline and forming a shallow arc concave anteriorly; epibranchials very conspicuous, curved; faint longitudinal ridge in midline from protogastrics to behind mesogastrics. Granular patches as follows: behind frontal ridges; relatively coarse granules, between protogastrics and mesogastrics; relatively fine, just behind inner terminations of epibranchial ridges;

diffuse patches in mesobranchial and cardiac areas; fine granules on bases of first to fifth anterolateral teeth, with patches on bases of second teeth the largest. Posterior part of cervical grooves deep, widely separated, distant from metagastric ridges.

CHELIPEDS: Long, spinous, upper surfaces sparsely hirsute, and slightly swollen, left slightly larger than right. Arm with anterior border bearing four spines which are curved, sharp and moderately robust; upper surface mostly coarsely granular; under surface smooth terminating in boss with sharp spine. Wrist with inner and three outer spines; inner spine of moderate length and sharp; carinae running to inner spine and to upper and lower of three outer spines. Upper surface of hand with four sharp, long spines including one at wrist articulation, one near centre of outer margin, and two on inner margin, one roughly at middle, one on distal border, carinae leading to inner and outer central spines, granular; outer surface with central carina a conspicuous ridge, above this distinct squamiform markings; under surface with hint of squamiform markings; inner surface with conspicuous central carina with a hint of squamiform markings above and below carina. Movable finger long, slender, deeply grooved. Immovable finger with inner and outer surfaces as in movable finger; under surface with shallow grooves.

WALKING LEGS: Moderately robust, for example carpus of last walking leg relatively short and broad.

FIFTH LEG: Merus elongate (see fig. 3); spine on posterodistal border. Propodus without spinules on posterodistal border (only one propodus available).

MALE ABDOMEN: Penultimate segment broader than long. Ultimate segment of moderate length.

MALE FIRST PLEOPOD: Sinuous, without obvious membrane. Subterminal armature: inner side, short but conspicuous bristles to aperture; outer side, relatively long row of long bristles.

PIGMENTATION (recently preserved specimen): Features common to all four species are separately listed (see p. 106). Distinctive features are: movable finger, upper, inner and outer surfaces, proximal one-third mostly pale pink, distal two-thirds red. Immovable finger, outer surface proximal one-third cream, distal two-thirds red, this extending slightly backwards, but not to level of articulation of movable finger; inner surface, proximal one-quarter to one-third mostly cream, with oblique separation from pink distal area.

COMMENTS

This species differs considerably from the remainder, and possesses the following distinctive features apart from pigmentation:

(1) Frontal teeth very acute and pointed, medians separated by deep angular fissure, separated from submedians by broad deep fissure.

- (2) Inner supraorbital angles sharp and acutely pointed.
- (3) Anterolateral teeth generally, very sharp-tipped, becoming sharper and more slender from second to fifth.
- (4) Relatively conspicuous but short frontal ridges.
- (5) Mesogastric ridges sinuous and almost bow-shaped.
- (6) Metagastric ridges forming shallow arc concave anteriorly.
- (7) Cheliped hand with long spines on upper surface.
- (8) Cheliped, immovable finger, under surface with shallow grooves.
- (9) Male first pleopod, subterminal armature, outer side relatively long row of long bristles.

It is known only from the type locality.

DISCUSSION

The four species belong to the subgenus *Charybdis* de Haan, 1833, in the sense used by Leene (1938, p. 18). Leene listed the characteristic features as:—

- (1) Whole of external angle of basal antennal joint joins the front and excludes flagellum from the orbit.
- (2) Margin of posterior border of cephalothorax forms a curve with posterolateral borders.
- (3) Six anterolateral teeth (seven if one is a small spine).
- (4) No spine on posterior border of arm of cheliped.
- (5) Four median frontal teeth not very dissimilar from lateral frontal teeth. This does not strictly apply to the present species in which the lateral teeth are narrower and more pointed than the medians or submedians. Because the affinities of the species are clearly with the other species of this "subgenus", it is best to eliminate this as a characteristic feature.

All species are without transverse ridges on the carapace behind the last anterolateral teeth and the first tooth is more or less truncate. This brings them into an eight species "assembly" which includes *C. feriatus* (L., 1758) = *C. cruciata* (Herbst), *C. japonica* (A. Milne Edwards, 1861), *C. affinis* Dana, 1852, and *C. rosaea* (Jacquinot, 1852).

Leene separated these species primarily on the number of spines on the anterior border of the arm. In the present species this has been shown to be variable, and a different basis for separation is required. The number of spines upon the hand is a convenient keying feature, with five species having four spines including that at wrist articulation (present four species and C. feriatus), two species having five spines (C. japonica and C. affinis) and one species having three spines (C. rosaea).

C. rosaea differs in numerous other respects from the remainder including a very narrow carapace, few spines on anterior border of arm of cheliped, and very short meri of fifth legs.

C. affinis and C. feriatus differ in several respects from the remainder including more swollen hands of chelipeds, smaller spines on chelipeds, more rounded and broader lateral frontal teeth, and broader and less claw-like second to fifth anterolateral teeth. However C. feriatus shows certain resemblances to C. riversandersoni including smoothness of carapace and relative inconspicuousness of its granular ridges.

Meanwhile *C. japonica* is reasonably close to *C. miles*, sharing with it a pilose carapace and chelipeds, relatively acute frontal teeth, meri of the fifth legs of approximately similar proportions and somewhat similar male first pleopods. In addition to having five instead of four spines on the upper surface of the hand of the cheliped, *C. japonica* has three as against four spines on the anterior border of the arm, relatively narrow median frontal teeth which are orientated forwards, relatively broader carapace, relatively smaller first anterolateral teeth, and stouter walking legs.

Apart from the "subgeneric" features, and those of the eight species "assembly" the features common to the four present species are:—

FRONT: Submedian teeth inclined laterally, lateral teeth more pointed and narrower than medians and submedians, outer supraorbital fissure barely open, general suborbital border granular.

ANTEROLATERAL TEETH: First relatively short with truncate, sometimes almost bifid margin; second to fifth broad-based, sharp-tipped, with anterior borders concave.

CHELIPEDS: Spinous, hand at least slightly swollen. Arm with anterior border bearing 3–5 sharp, curved spines. Under surface terminating distally in boss with spine or tubercle. Wrist with well-developed inner spine and in unworn specimens three outer spines; carinae run to inner spine and to upper and lower of the three outer spines. Upper surface of hand with four spines including one at wrist articulation, one near centre of outer margin, and two on inner margin, one roughly at middle, one on distal border; outer surface with distinct central carina and above this at least a tendency to squamiform markings.

FIFTH LEG: Spine on posterodistal border of merus.

THIRD MAXILLIPED: Anteroexternal angle of merus distinctly expanded in lateral direction.

MALE ABDOMEN: Penultimate segment broader than long. Ultimate segment triangular with rounded tip.

MALE FIRST PLEOPOD: Sinuous, without obvious membrane. Subterminal armature on inner side with bristles to aperture.

PIGMENTATION (in recently preserved specimens): Carapace with light area in postlateral regions. Cheliped, upper surfaces of arm and hand pink with light mottling; outer surface of hand with vertical pink bars reminiscent of squamiform arrangement of granules; fingers, distal halves of inner surfaces of movable and immovable fingers pink or red; ends of fingers mostly dark brown with paler tips.

All the above features were included in the specific descriptions except the colour features held in common.

Of the four species *C. miles* and *C. rufodactylus* are each distinguished by numerous features as listed and are not likely to be confused. On the other hand *C. riversandersoni* and *C. sagamiensis* resemble each other in numerous features as follows:—

- (1) Median and submedian frontal teeth relatively stout.
- (2) Median frontal teeth separated by moderately deep to deep fissure, pointing directly forwards, and slightly narrower than submedians.
- (3) Carapace relatively broad and hairless.
- (4) Branchial regions of carapace at least faintly swollen.
- (5) Posterior part of cervical grooves distant from metagastric region.
- (6) Chelipeds, arm, with under surface smooth.
- (7) Chelipeds, hand, with carinae on inner and outer surfaces rounded ridges.
- (8) Chelipeds, hand, inner surface smooth above and below carina.
- (9) Chelipeds immovable finger, inner and outer surfaces moderately deeply grooved, undersurface smooth and rounded.

C. riversandersoni and C. sagamiensis differ in:-

- (1) Median and submedian frontal teeth less sharply triangular in *C. riversandersoni*.
- (2) Fissure between median and submedian frontal teeth broader in *C. river-sandersoni*, deeper in *C. sagamiensis*.
- (3) Submedian frontal teeth more inclined laterally in C. riversandersoni
- (4) Fissure between submedian and lateral frontal teeth broader in *C. rivers-andersoni*, deeper in *C. sagamiensis*.
- (5) Inner supraorbital angles stouter in C. riversandersoni.
- (6) Inner supraorbital fissure more widely open in C. riversandersoni.
- (7) First anterolateral tooth narrower in C. riversandersoni.
- (8) Anterolateral teeth, with second relatively short, third and fourth relatively broad, fifth relatively sharp and protruding in *C. riversandersoni*.

- (9) Sixth anterolateral tooth shorter and less upwardly directed, and curved forwards in *C. riversandersoni*.
- (10) Branchial regions of carapace more swollen in C. riversandersoni.
- (11) Carapace ridges less strongly developed in C. riversandersoni.
- (12) In *C. riversandersoni* metagastric ridges very widely separated in midline and barely recognisable; in *C. sagamiensis* metagastrics moderately separated in midline, and almost straight.
- (13) Epibranchial ridges less conspicuous and less curved in C. riversandersoni.
- (14) Smooth carapace in *C. riversandersoni*, fine diffuse granular patches present on carapace in unworn specimens of *C. sagamiensis*.
- (15) Posterior part of cervical grooves deeper and less widely separated in *C. riversandersoni*.
- (16) Chelipeds, less massive in C. riversandersoni.
- (17) Chelipeds, upper surfaces hairless in *C. riversandersoni*, with few hairs in *C. sagamiensis*.
- (18) Chelipeds, arm, upper surface smooth in *C. riversandersoni*, mostly very finely granular in *C. sagamiensis*.
- (19) Chelipeds, wrist, inner spine stouter in C. riversandersoni.
- (20) Chelipeds, wrist, carina running to inner spine more obscure in *C. rivers-andersoni*.
- (21) Chelipeds, hand, outer surface above carina with less conspicuous squamiform markings in *C. riversandersoni*.
- (22) Chelipeds, hand, under surface smooth in *C. riversandersoni* as against with faint squamiform markings in *C. sagamiensis*.
- (23) Chelipeds, movable finger longer and more slender in C. riversandersoni.
- (24) Walking legs relatively more slender in C. riversandersoni.
- (25) Fifth leg, merus more elongate in C. riversandersoni.
- (26) Male abdomen ultimate segment relatively longer in C. riversandersoni.
- (27) Male first pleopod: outer side without concentration of bristles just behind tip in *C. riversandersoni*.

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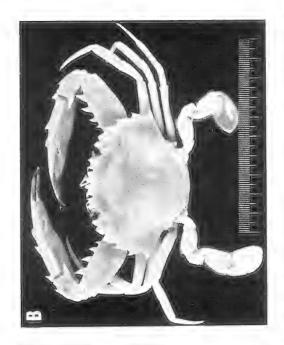
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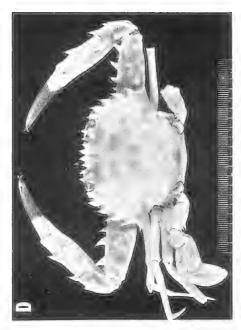
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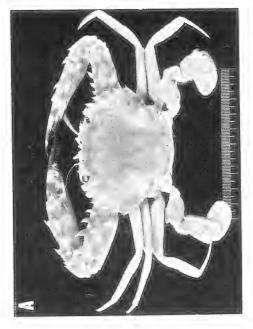
PLATE 12

Dorsal views. Scale 1 div. = 1 mm.

- A. Charybdis miles
- B. C. riversandersoni
- C. C. sagamiensis
- D. C. rufodactylus











THE IDENTITY OF THE EXTINCT MARSUPIAL GENUS NOTOTHERIUM OWEN

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ABSTRACT

As a basis for the clarification of the taxonomy of the genus *Nototherium* Owen (Marsupialia: Diprotodontidae) a lectotype for the type species *N. inerme* Owen is selected. *N. mitchelli* Owen and *Euowenia robusta* De Vis are treated as junior synomyms of this name.

It has already been pointed out by Stirton (1955) that in the literature of Australian fossil marsupials the generic name *Nototherium* is second only to *Diprotodon* in frequency. Unfortunately both species included by Owen (1845 a, b) in the genus at the time of its description were based on poor material and their subsequent interpretation has been far from satisfactory.

The present paper is a contribution to the discrimination of these taxa, and has resulted from a study over several years of the large collection of Diprotodontidae in the Queensland Museum, including much fragmentary material, as well as specimens in other repositories. This has been carried out through the courtesy of Mr. H. O. Fletcher, Australian Museum, Sydney, Mr. E. D. Gill, National Museum of Victoria, Melbourne, and Dr. A. J. Sutcliffe, British Museum (Natural History), London. It is also desired to acknowledge with gratitude profitable discussion with Mr. Alan Bartholomai, Queensland Museum, Brisbane, and Dr. W. D. L. Ride, Western Australian Museum, Perth. The photographs of the type of *N. mitchelli* were kindly furnished by Dr. Ride.

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THE TYPE SPECIES OF NOTOTHERIUM

Owen (1845a) published the generic name *Nototherium* and the species names *N. inerme* and *N. mitchelli* in the *Report of the Fourteenth Meeting of the British Association*. It is held that in this work *N. mitchelli* has only the status of a *species inquirenda*, since Owen (p. 233) states "The difference in the shape, as well as the size of the jaw, bespeaks at least a specific distinction from the jaw referred to *Nototherium inerme*." The names were also published in the "Descriptive and Illustrated Catalogue of the Fossil Organic Remains of Mammalia and Aves Contained in the Museum of the Royal College of Surgeons of England" (Owen, 1845b), and the doubtful generic position of *N. mitchelli* is again indicated in his discussion on No. 1506, its type, in which he states "The difference of the shape, as well as the size of the jaw, bespeaks at least a specific distinction from No. 1505." The latter is the holotype or a syntype of *N. inerme*, depending on the priority of the respective publications.

However, no matter which publication has priority, it is clear that the genus *Nototherium* was established with one certain nominal species, *N. inerme;* the other, *N. mitchelli*, having been included with some doubt on both occasions. The type species is therefore *N. inerme* by monotypy.

Subsequently Owen (1877) indicated that he considered *N. mitchelli* as the type species. He states (p. 275) "Of *Nototherium inerme* I have the entire molar series of both sides of the upper jaw; with sufficient of that part of the skull to demonstrate its generic accordance with the more complete specimen of the skull of the type-species in the Museum at Sydney." This latter specimen, a cranium, is the holotype of *Zygomaturus trilobus* Macleay, which Owen had regarded (1873) as conspecific with a mandible he had identified as *N. mitchelli*. It will be argued that Owen misinterpreted *N. mitchelli* in this paper, and the confusion in the application of the name stemmed from then. Flower (1884) and Lydekker (1887) treated *N. inerme* as a junior synonym of *N. mitchelli*.

While Longman (1921) did not accept this synonymy, he formally proposed *N. mitchelli* as the type species, apparently unaware of Owen's (1877) statement, and in the belief that he was confirming Lydekker's action in treating it as the type species.

However, in view of the doubtful generic status attributed by Owen (1845a, b) to N. mitchelli at the time of its original proposal, neither Owen's nor Longman's subsequent designation of it as the type species invalidates the situation whereby N. inerme has been automatically the type species of Nototherium from its time of publication.

THE TYPES OF N. inerme AND N. mitchelli

N. INERME

Owen (1845a) described as the "principal fossil", an incomplete right ramus, with evidence of four molar teeth and portion of the symphysis. He believed the incisors had not been developed. The specimen was not figured.

This is certainly the same specimen listed as No. 1505, and described and figured (Owen 1845b, plate 8, figs 1–5). It is stated to have been derived "From the alluvial or newer tertiary deposits in the bed of the Condamine River, west of Moreton Bay, Australia" and "Presented by Lieut.-Col. Sir T. L. Mitchell, C.B.". A second specimen listed as No. 1507 from the same source, consisting of smaller portion of a right ramus, with remains of the last two molars was attributed to *N. inerme*, but not figured.

Should the "Catalogue" have priority both specimens are to be regarded as syntypes of *N. inerme*. When Owen (1873) subsequently discussed the genus *Nototherium* in some detail it is clear that he regarded No. 1505 as the type of *N. inerme*. However, it may never be possible to ascertain with complete certainty which of the two publications is the earlier and for this reason it is deemed desirable to designate as the lectotype No. 1505, described and figured by Owen (1845b, pp. 314–6, pl. 8, figs 1–5). In the subsequent illustration of Owen (1873, pl. 8, figs 1–4) of this specimen it has been grossly restored. It is listed by Flower (1884) as No. 3844 under *N. mitchelli*.

This specimen is believed to have been destroyed when the Museum of the Royal College of Surgeons was bombed in 1941, but Owen's (1845b) description and figures are sufficient for the discrimination of the species.

N. MITCHELLI

Since the name was based only on one fossil in the original descriptions, this specimen is automatically the holotype. It consists of an incomplete posterior half of a left ramus, with the third and fourth molars imperfectly preserved, and was listed by Owen (1845b) as No. 1506, described, and figured (pl. 9, figs 1–5). Subsequently Flower (1884) listed it as No. 3843 in the collection of the Royal College of Surgeons. It is now preserved as M.16590 in the collections of the British Museum (Natural History).

THE INTERPRETATION OF THE SPECIES AND SYNONYMY

With such imperfect type material it becomes necessary to interpret the species to which they belong, essentially on the basis of referred specimens, which as individuals can be compared directly with the types only in a small number of characters, or sometimes only indirectly.

In the type of N. inerme (plate 13, figs 1, 2) the available characters are (1) the size of the ramus; (2) the size of the teeth; (3) the shape of the ramus particularly the degree of curvature of the ventral margin as seen in lateral view and the rather steep ascent of this margin behind the diagastric process; (4) the height of the dental foramen relative to the postalveolar shelf; (5) the development of the diagastric process; and (6) the depth of the alveolus for the incisor.

In the type of N. mitchelli (plate 13, figs 3-5) the available characters are (1), (2), (3), (4), (5) as above, and (7) the configuration of the molar crowns.

The depth of implantation of the fourth molar in the type of N. inerme shows that the fossil was derived from an immature individual with this tooth incompletely erupted. Because of immaturity the molar row had not progressed forward and the postalveolar shelf is short. In contrast, while the molars of the type of N. mitchelli are broken and very incomplete, sufficient of their surface is retained to indicate that wear on the posterior molars was at an advanced stage and the individual was mature. Similarly the length of the postalveolar shelf points to considerable progression of the molar row. The interpretation of Owen (1845a, p. 233; 1845b, p. 317) that both were mature specimens is therefore disputed.

Taking the difference in maturity into account, it is immediately apparent that there is close agreement in characters (1)-(5) in both jaws. This agreement is reinforced by individual comparison with material of *Euowenia robusta* De Vis (plate 14, figs 1-3), including the type, in the collections of the Queensland Museum. The three taxa are regarded as conspecific, with *Nototherium mitchelli* Owen and *Euowenia robusta* De Vis, 1891 as junior synonyms of *Nototherium inerme* Owen.

While the presentation of revised diagnoses for the genus *Nototherium* Owen and its type species are beyond the scope of this preliminary paper, it may be said that that for the species includes the following characters of the mandible pertinent to the preceding discussion. The ramus and molar teeth are those of a medium-sized diprotodontid; in lateral view the ventral margin of the body of the ramus is gracefully curved and, beyond the diagastric process which is relatively weak even in aged individuals, it ascends steeply; the dental foramen is markedly elevated above the plane of the postalveolar fossa; the lophids of the molars are obliquely crescentic and the median valley is closed at the base by a weak but persistent midlink descending from the middle of the protolophid, to meet the stronger link from the hypoconid. The presence of the part of the midlink descending from the protolophid may be observed in the type of *N. mitchelli*.

Owen (1845a, b) supposed that the incisor teeth in *N. inerme* were lacking altogether and in fact it appears that the symphysial region of the type is broken in the vicinity of the base of the incisor alveolus. In this species the lower incisors are

subconical, anteriorly divergent and the base of the alveolus for each incisor extends to beneath the premolar; but the depth of implantation is somewhat variable as in all diprotodontids and this last character is of no great significance.

The only diprotodontid names published before 1845 are *Diprotodon optatus* Owen, 1838 and *Dinotherium australe* Owen, 1843. The holotype of *D. optatus* is the anterior portion of a right mandibular ramus with a broken incisor preserved as number M. 10796 in the collections of the British Museum (Natural History). The form of the incisor is such that the fossil cannot be conspecific or even congeneric with *N. inerme* as interpreted above. The holotype of *Dinotherium australe* has large molars with transverse lophids (Owen, 1843, figs 1–2) and again there is clear generic distinction from *N. inerme*.

Nototherium Owen is therefore considered to be a valid generic name and N. inerme Owen a valid and viable species name. The relegation of N. mitchelli to synonymy should have the result of preventing further confusion of its application, which stemmed from Owen's misidentification of material when he revised the genus Nototherium (1873). The extent of this may be gauged by reference to the specimens figured in the plates of this work:

- (1) The cranium illustrated on Plates 2 and 3 as N. mitchelli relates to Zygomaturus trilobus Macleay.
- (2) The mandible illustrated on Plate 4 as N. mitchelli relates to Z. trilobus.
- (3) The mandible illustrated on Plate 5 as N. mitchelli relates to N. inerme.
- (4) The mandible illustrated on Plate 6 as N. mitchelli relates to Z. trilobus.
- (5) The mandible illustrated on Plate 7 as N. victoriae may be attributed to Zygomaturus.
- (6) The mandible illustrated on Plate 8 is the holotype of *N. inerme* grossly restored.
- (7) The upper cheek teeth illustrated on Plate 9, figs 3–4, as *N. mitchelli* relate to *Z. trilobus*.
- (8) The upper cheek teeth illustrated on Plate 9, fig. 5, as *N. inerme* are correctly identified.
- (9) The lower cheek teeth illustrated on Plate 10 as N. mitchelli and N. victoriae relate to species of Zygomaturus.
- (10) The incomplete ramus illustrated on Plate 11 as N. mitchelli relates to Euryzygoma dunense (De Vis).

There has been very little usage of the name *Euowenia robusta* De Vis since the time of its original description (De Vis, 1891) so the present synonymy cannot be said to upset stability in that regard. The type species of the genus is *E. grata* De Vis, and on this basis the relation of *Euowenia* to *Nototherium* becomes a matter for further consideration.

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PLATE 13

Nototherium inerme; all one-third natural size.

- Fig. 1: Occlusal view of lectotype of N. inerme Owen; reproduced with permission of the Royal College of Surgeons from Owen (1845b) (reversed as in original).
- Fig. 2: Lingual view of lectotype of N. inerme; as above.
- Figs 3, 4: Stereo pair of occlusal view of holotype of N. mitchelli Owen.
- Fig. 5: Labial view of holotype of N. mitchelli Owen.

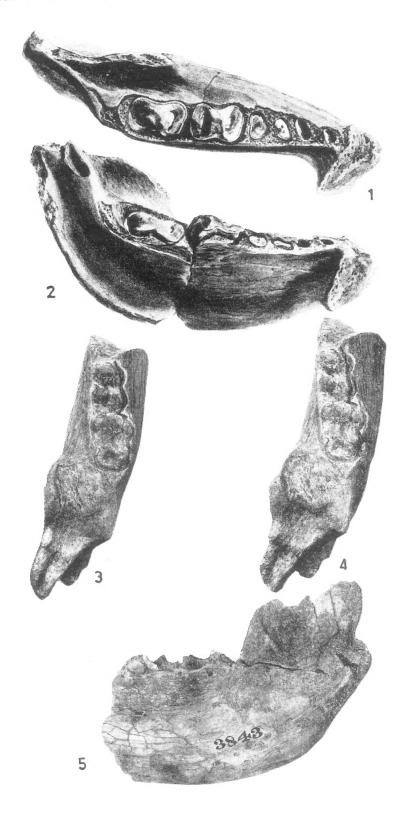


PLATE 14

Nototherium inerme; all one-third natural size.

- Fig. 1: Occlusal view of holotype of *Euowenia robusta*De Vis; F. 517, Queensland Museum collection,
 from Pleistocene alluvium along Freestone Creek,
 Darling Downs, S.E.Q.
- Fig. 2: Labial view of holotype of E. robusta.
- Fig. 3: Occlusal view of F. 522, Queensland Museum collection; specimen from Darling Downs, S.E.Q., showing more complete molars.



CONTENTS

	Page
Armstrong, J. D. and Brown, C. D.	
A New Species of Attenuatella from the Permian of Queensland	59
BARTHOLOMAI, ALAN	
A New Fossil Koala from Queensland and a Reassessment of the Taxonomic Position of the Problematical Species, Koalemus ingens De Vis	65
CROSBY, ELEANOR	
An Archaeological Site Survey near Taroom, South-Eastern Queensland	73
Stephenson, W.	
Variability in the Sand Crab Portunus pelagicus (Linnaeus) (Crustacea: Portunidae)	83
STEPHENSON, W. and REES, MAY	
A Revision of the Charybdis miles "Group" of Species (Crustacea: Portunidae), with Description of a New Species from Queensland Waters	91
Woods, Jack T.	
The Identity of the Extinct Marsupial Genus Nototherium Owen	111